Comparative Basicranial Anatomy of Extant Terrestrial and Semiaquatic Artiodactyla

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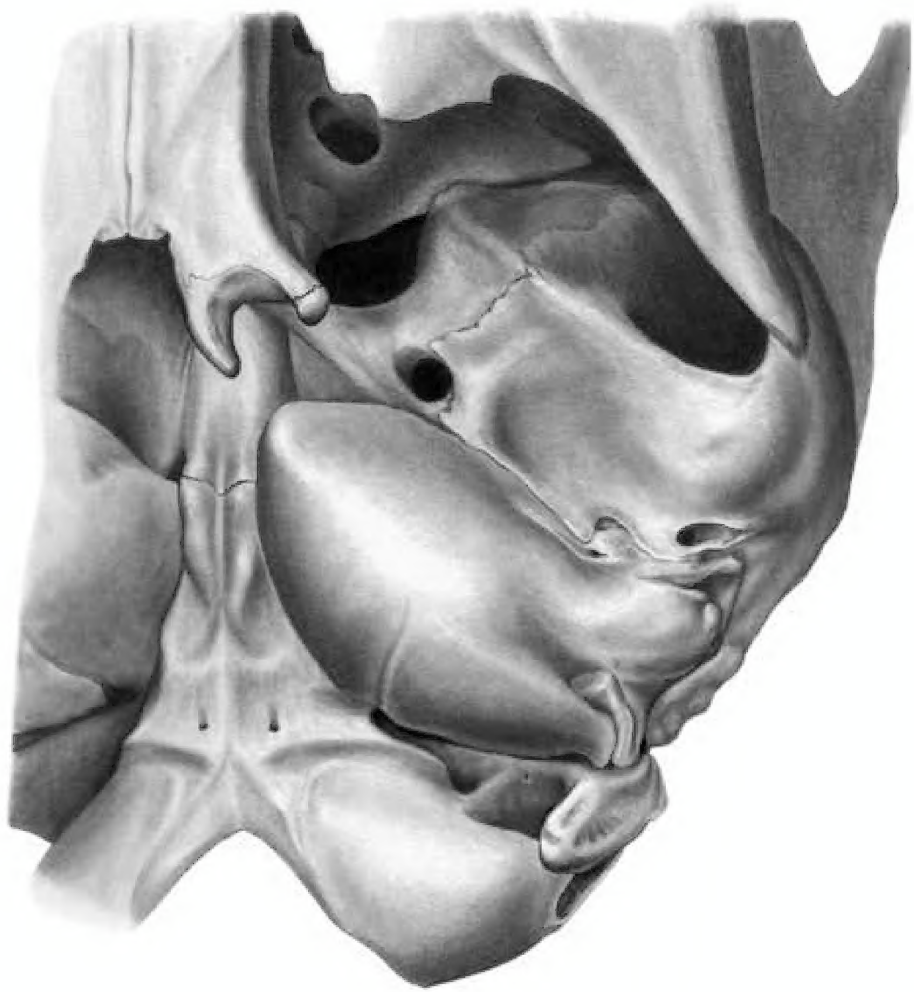

Bulletin of the American Museum of Natural History

COMPARATIVE BASICRANIAL ANATOMY OF EXTANT TERRESTRIAL AND SEMIAQUATIC ARTIODACTYLA

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CONTENTS

Abstract 3
Introduction 3
Explanations of Certain Anatomical Terms 6
Institutional Abbreviations 9
Basicranial Descriptions 9
Camelidae 9
Camelus dromedarius 9
Suina – Tayassuidae 15
Pecari tajacu and *Tayassu pecari* 15
Suina – Suidae 19
Potamochoerus porcus 19
Babyrousa babyrussa 23
Cetruminantia – Ruminantia – Pecora – Bovidae 28
Bos taurus 28
Cetruminantia – Ruminantia – Pecora – Cervidae 31
Odocoileus virginianus 31
Cetruminantia – Ruminantia – Tragulidae 36
Tragulus javanicus and *T. napu* 36
Cetancodonta – Hippopotamidae 41
Choeropsis liberiensis 41
Hippopotamus amphibius 44
Comparative anatomy 48
Conclusions 53
Acknowledgments 53
References 54

ABSTRACT

Comparative data from the ear region has played an important role in recent combined-data phylogenetic analyses of the relationships of living and extinct Artiodactyla and the position of that clade among Euungulata. These studies have also been important for establishing the phylogenetic position of Cetacea and for understanding the relationships of a diversity of euungulate species to their fossil relatives. Detailed and standardized descriptive reference works of the basicranium for a range of living artiodactylans are not, however, readily available. Here I describe exemplar species from the four major extant terrestrial and semiaquatic artiodactylan clades (Hippopotamidae, Ruminantia, Suina, and Camelidae) and illustrate the anatomy of the ear region with the auditory bulla both in place and removed. Terrestrial artiodactyls exhibit varying degrees of expansion of the bony external acoustic meatus laterally relative to the mediolateral dimensions of the rounded, medial aspect of the auditory bulla, a characteristic that is least developed in Tragulidae. A relatively elongate external acoustic meatus has previously been described as entirely absent in living and fossil cetaceans and in some fossil species such as *Diacodexis pakistanensis*. Variation also exists in the proximity of the petrosal-bullar complex to midline basicranial bones. Isolation of these bones from other basicranial structures has been previously interpreted as functionally important for underwater hearing in Cetacea. Many artiodactylans have contact between the auditory bulla and the basioccipital but no contact between the deeper pars cochlearis of the petrosal bone and the basioccipital/basisphenoid. Exceptions are species of Hippopotamidae in which both the bulla and the petrosal are separated from midline bones. The functional interpretation of this separation has previously been linked to aquatic hearing, but this association may be more complex than originally thought. Other features observed in the basicrania of terrestrial artiodactylans described here are a general coalescence of basicranial foramina (i.e., the basicapsular fissure, carotid foramen, piriform fenestra, and sometimes the foramen ovale), the development of large and ornate styliform processes in species of Ruminantia, and widespread contact between the auditory bulla and the paracondylar process of the exoccipital.

INTRODUCTION

The middle ear region of the mammalian skull has been a rich source of characters for phylogenetic work (Archer, 1976; Coombs and Coombs, 1977; Novacek, 1986; Hunt, 2001; Wible, 2003; Giannini et al., 2006; Mead and Fordyce, 2009; O'Leary, 2010; O'Leary et al., 2013; Orliac, 2013) due in large part to the complex and variable nature of the petrosal bone, which forms the "roof" of the middle ear (specifically the medial and superior borders), and the associated auditory bulla, which forms its "floor" (ventral and lateral borders). For the study of many mammal species, access to the petrosal bone in situ in the skull is direct because the "floor" of the middle ear, the auditory bulla, which covers the petrosal (variably composed of different bones, including petrosal, ectotympanic, and entotympanic, among others), is loosely attached to the skull. The bulla is thus easily removed in a dry specimen revealing the underlying petrosal, its relationship to surrounding skull bones, and occasionally in situ ear ossicles. This arrangement is not the case for many noncetacean artiodactylans, which may have a petrosal or bulla that is tightly interlocked with surrounding bones. A ventral view of the petrosal in situ has become a standardized part of skull descriptions for mammalian taxa (Evans and Christensen, 1979; Webb and Taylor, 1980; Novacek, 1986; Luo and Gingerich, 1999; Giannini et al., 2006), and thus it is important to have such references for Artiodactyla. While a few recent reference texts have emerged for the noncetacean artiodactylan petrosal (O'Leary, 2010; Orliac et al., 2010; Orliac, 2013; Orliac and O'Leary, 2014) and the cetacean skull (Luo and Gingerich, 1999; Mead and Fordyce, 2009), no

standardized treatment of the skulls of extant artiodactylans, describing the relationship of the petrosal to surrounding bones across the clade, currently exists.

Anatomical research on the fossil and living clades of Euungulata (defined by O'Leary et al. [2013: 104, supplementary methods] as "the least inclusive clade of *Tursiops truncatus, Lama glama,* and *Equus caballus* and all of its descendants") has been important for understanding the origin of Cetacea, one of the key examples among vertebrates of a transition from terrestrial to aquatic habitat. Excepting Cetacea, the order Artiodactyla includes four major clades with extant members: Hippopotamidae, Suina, Camelidae, and Ruminantia. Recent combined data studies (Spaulding et al., 2009) have shown that these artiodactylan families are also clades (fig. 1), and that in all shortest trees, Hippopotamidae is the sister taxon of Cetacea, and Ruminantia is the outgroup to Hippopotamidae + Cetacea. Next down the tree is the clade Suina, and finally Camelidae is the sister clade of all other artiodactylans. These branching relationships are congruent with those found in a study of placental mammal relationships using combined data that included many more characters that were sampled for fewer extant and extinct species (O'Leary et al., 2013).

A recent comprehensive basicranial description of an exemplar odontocete cetacean (*Tursiops truncatus*) provides a key anatomical resource for part of the artiodactylan clade (Mead and Fordyce, 2009). For noncetacean artiodactylans, however, descriptions and illustrations of the ventral view of the petrosal in situ are uncommon because, as noted above, the auditory bulla and petrosal may be tightly fused in place. Here I describe and illustrate the petrosal in situ in a variety of extant artiodactylans from which the bulla has been removed through destructive sectioning (table 1). Relationships among artiodactylan clades have been researched elsewhere (Spaulding et al., 2009; O'Leary et al., 2013), as have aspects of the functional morphology of this anatomical region in the clade (Luo and Gingerich, 1999; O'Leary et al., 2012). By comparing eight taxa for one anatomical region, variation in homologous structures can be readily identified and discussed.

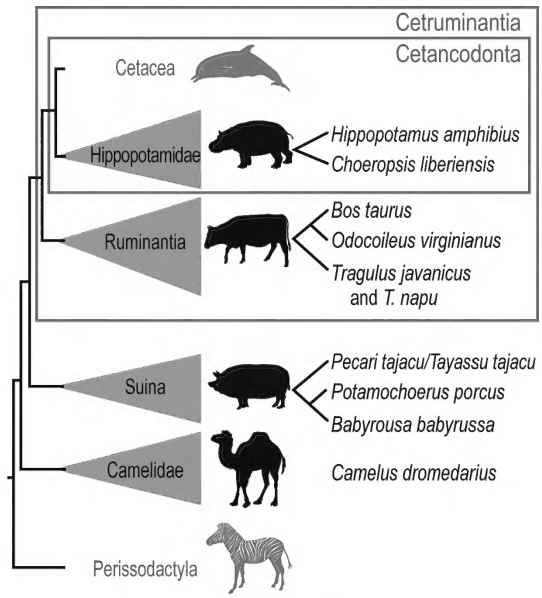

FIGURE 1. Tree of the interrelationships of extant clades of Artiodactyla based on the combined-data analyses of Spaulding et al. (2009) and O'Leary et al. (2013). Clade names as defined in Spaulding et al. (2009). Species listed on the right are those illustrated here (table 1).

It can be difficult to show the complex features of the petrosal itself while simultaneously showing its relationship to surrounding basicranial bones. O'Leary (2010) figured multiple views of the petrosals of all taxa described here and readers are referred to that source for more detailed discussion of that bone. A few structures on the petrosal are indicated in this publication when necessary for orientation. If visible in the drawings, other anatomical features of the adjacent palate, nasal, and jaw joint regions are also noted. Other important recent (Gurr et al., 2010) and classic (Smuts and Bezuidenhout, 1987) publications have contributed excellent new illustrations of delicate soft-tissue ear structures in artiodactylans.

The species described here are phylogenetically positioned across Artiodactyla (except Ceta-

TABLE 1

List of specimens of Artiodactyla used in this study.
Choeoropsis specimen not available for bulla removed.

Clade	Taxon	Specimen number (bulla in situ)	Specimen number (bulla removed and/or bulla in isolation)	Supplementary specimens
Cetruminantia Ruminantia Pecora Bovidae	*Bos taurus*	SBU MAR 15	SBU MAR 14	
Cetruminantia Ruminantia Pecora Cervidae	*Odocoileus virginianus*	AMNH-M 244789	SBU MAR 20	
Cetruminantia Ruminantia Tragulidae	*Tragulus javanicus*		AMNH-M 102091	
Cetruminantia Ruminantia Tragulidae	*Tragulus napu*	AMNH-M 188310		
Cetruminantia Ruminantia Tragulidae	*Tragulus sp.*			AMNH-M 32652
Camelidae	*Camelus dromedarius*	AMNH-M 14111	SBU MAR 31	AMNH-M 6368
Cetancodonta Hippopotamidae	*Choeropsis liberiensis*	AMNH-M 81899	UCR 3116	AMNH-M 148452
Cetancodonta Hippopotamidae	*Hippopotamus amphibius*	USNM-M 182395	USNM-M 182395, AMNH-M 24289	USNM-M 162981
Suina Suidae	*Babyrousa babyrussa*	AMNH-M 152858	AMNH-M 2238	AMNH-M 152861
Suina Suidae	*Potamochoerus porcus*	AMNH-M 238330	AMNH-M 53703, AMNH-M 238329	AMNH-M 100670
Suina Tayassuidea	*Tayassu pecari*	SBU MAR 8		AMNH-M 133513
Suina Tayassuidea	*Pecari tajacu*		UCM-VZ 1247	

cea), and are among those for which petrosal anatomy has been described and illustrated in O'Leary (2010) and scored in Spaulding et al. (2009). I describe two species of Hippopotamidae, three species of Ruminantia, three species of Suina, and one species of Camelidae. This choice of specimens does not necessarily capture all the anatomical variation in these clades, but serves to document the morphology that underlies ongoing large-scale tree-building efforts. For example, information below indicates that there are minimal significant differences between *Babyrousa* and *Potamochoerus* in the features discussed for the ear region anatomy, however, both are described because there is little detail in the existing literature for either species to serve as a resource documenting phylogenetic scoring.

I provide a self-contained description for each taxon, first of the basicranial region (including brief details about the orbit) with the bulla in situ. Then I discuss additional features of the basicranium visible with the bulla removed (including some notes on the glenoid fossa due to its proximity to the middle ear), and describe features of the bulla that are exposed upon its separation from the skull. The last section of the paper compares basicranial variation of the eight exemplar taxa, primarily in the context of the Spaulding et al.'s (2009) cladistic analysis of Artiodactyla due to its relatively large taxon sample, with notes on the results of O'Leary et al. (2013). Spaulding et al. (2009) also included many extinct members of Pan-Euungulata (the total clade of Euungulata

[O'Leary et al., 2013]). Higher-level taxonomy used in this paper follows the phylogenetic clade names defined by Spaulding et al. (2009) and O'Leary et al. (2013), who defined clades more inclusive than the level of family as either stem or total clades.

Explanations of Certain Anatomical Terms

Anatomical terms used here follow the synthetic definitions for mammalian cranial anatomy outlined by O'Leary et al. (2013). I briefly discuss some of these terms as applied to Artiodactyla (see also table 2). The cranial partition of the character matrix of O'Leary et al. (2013), as available in MorphoBank (O'Leary and Kaufman, 2007; O'Leary and Kaufman, 2011), Project 773, includes detailed notes and explanations of homology, and was curated and annotated by another author of that paper, John Wible, with input from numerous other authors (see O'Leary et al., 2013: supplementary methods). That paper also synthesized and standardized terminology from numerous descriptive texts including those on Artiodactyla (Pearson, 1927; Webb and Taylor, 1980; Janis and Scott, 1987; Luo and Gingerich, 1999; Mead and Fordyce, 2009). To continue to build a consistent lexicon for mammalian comparative anatomy, I follow the terms described by O'Leary et al. (2013) and incorporate information from papers on Artiodactyla published subsequently (Orliac et al., 2014; Orliac and O'Leary, 2014; Rakotovao et al., 2014). Further descriptions, definitions, and references for the anatomical terminology used here can be found on MorphoBank in the matrix of Project 773.

In Artiodactyla, the auditory bulla has been hypothesized to be ecotympanic in origin (Kampen, 1905; Klaauw, 1922; Novacek, 1977; Wible, 1984), however, Wible (1984) discusses reports of the presence of other bony elements. My descriptions here provide no new comparative embryological data on the bulla, the true composition of which is generally unknown for the large majority of fossils for which there are no known growth series. While acknowledging this compositional homology issue here, for simplicity, I refer to the bulla as ectotympanic throughout. The ectotympanic extends laterally as the ventral floor of the external acoustic meatus in some species, including members of Artiodactyla (homology discussed by Luo and Gingerich, 1999). Suina and Hippopotamidae in particular also tend to have a very elongate external acoustic meatus (Pearson, 1927; 1929; Rakotovao et al., 2014), a condition that Pearson (1927: 394) has called the "tympanic 'neck,'" which she noted is often accompanied by extensive fusion of the bulla to the squamosal. Kampen (1905) stated that even with this elongate condition, the ventral part of the wall of the entire external acoustic meatus is most likely composed of ectotympanic. Fusion complicates differentiation of the bony components of the external acoustic meatus in adult specimens. Thus, in the illustrations of the isolated auditory bullae that follow below, in taxa in which there is both extreme elongation and fusion, the composition of the ventral floor of the bony external acoustic meatus is not specified as it could be either squamosal or ectotympanic.

The ectotympanic bulla has posterior and anterior openings on its medial side that would have allowed passage in life for the internal carotid nerve and artery (if present) traveling from the deep neck to the middle ear and anteriorly to enter the cranial cavity. These openings into and out of the bulla are called the posterior and anterior carotid foramina, respectively (see MorphoBank Project 773, O'Leary et al., 2013: char. 446, for further discussion and synonyms). In Artiodactyla, neither the anterior nor the posterior carotid foramen is completely enclosed by bulla alone. The bulla may have a semicircular indentation that forms a foramen only when it meets the skull base, typically at the petrosal bone. In the species described here there is also no canal internal to the bulla between these foramina; any soft-tissue structures traveling between the bullar openings exist within the middle ear itself. After structures exit the middle ear anteriorly via the anterior carotid foramen, a separate named open-

TABLE 2

Anatomical terms used in this study.

Items in **boldface** are names of bones, those in regular typeface are structures on bones or soft tissues.

Structure or bone	Bulla in situ	Bulla removed
accessory foramen	x	x
alisphenoid	x	x
alveolar line		
anterior carotid foramen	x	
auditory bulla	x	
auditory tube sulcus	x	x
auditory tube		
basicapsular fissure		x
basipharyngeal canal	x	x
basioccipital	x	x
basisphenoid	x	x
bullar ridge	x	
carotid foramen/incisure	x	x
caudal tympanic process of petrosal		
condyloid canal	x	x
craniopharyngeal canal	x	x
ectotympanic annulus (with anterior crus and posterior crus)		x
ectopterygoid process	x	
endocranium		
entopterygoid process	x	
epitympanic wing of petrosal		x
exoccipital	x	x
external acoustic meatus (ectoympanic and squamosal portions)	x	x
fenestra cochlea		x
fenestra vestibuli		x
flexion stops	x	x
foramen magnum	x	x
foramen/incisura ovalis	x	x
frontal	x	x
frontal process of the jugal	x	
glenoid fossa	x	x
hamulus	x	x
hypoglossal foramen	x	x
hypoglossal foramen (accessory)	x	x
internal carotid artery		
internal carotid nerve		
internal carotid plexus		
internal jugular vein		
jugal	x	x
jugular foramen/incisure	x	x
major palatine foramen	x	
mastoid region of petrosal	x	
meatal foramen	x	
medial glenoid pit	x	
median crest		x
middle ear	x	x
middle lacerate foramen	x	x
minor palatine foramen	x	x
occipital condyle	x	x
occipital ridge	x	
optic foramen	x	
palatine	x	
paracondylar process of the exoccipital	x	
parietal	x	x
pars canalicularis of petrosal		x
pars cochlearis of petrosal		x
petrosal	x	x
petrotympanic fissure		
piriform fenestra	x	x
porus acusticus externus	x	
posterior carotid foramen	x	
posterior spine	x	
posteromedial flange of the petrosal		x

Table 2. *continued*

Structure or bone	Bulla in situ	Bulla removed
postglenoid foramen	x	x
postglenoid foramen (accessory medial or lateral openings)	x	x
postorbital process of the frontal	x	
postglenoid process of squamosal	x	x
postorbital process of the frontal	x	x
preglenoid process of squamosal	x	x
posttympanic process of the squamosal	x	x
presphenoid	x	
promontorium		x
pterygoid	x	x
pterygoid fossa		
pterygoid canal anterior opening		
pterygoid canal posterior opening	x	x
rostral tympanic process	x	
secondary facial foramen		x
sphenorbital fissure	x	
squamosal	x	x
styliform process	x	
stylohyal fossa	x	
stylomastoid foramen/notch	x	
sulcus to pterygoid canal	x	x
suture	x	x
tegmen tympani		x
third molar	x	x
tympanic process	x	x
tympanohyal	x	
vomer	x	

ing into the mammalian braincase , the carotid foramen (see below), permits passage of soft-tissue structures exiting the middle ear to the inside of the skull. Many members of Artiodactyla have been reported to have a small or obliterated internal carotid artery in the adult, even if this vessel is patent in some juveniles (Wible, 1984; Geisler and Luo, 1998; Fukuta et al., 2007; O'Brien, 2015, and references therein; see also discussion below); thus, for this clade, the course of soft-tissue structures described above, may be taken primarily by the internal carotid nerve.

Immediately lateral to the anterior carotid foramen is the auditory tube opening (musculotubal canal of Evans and Christensen, 1979), a channel between the middle ear and the nasopharynx. The auditory tube opening tends to be similar in size to the anterior carotid foramen and also exists as a variable indentation in the bulla that forms a canal only when it meets the skull base (i.e., the petrosal bone) superiorly. The bony auditory tube and the anterior carotid foramen are not always distinct in Artiodactyla, but the bony auditory tube is often marked ventrally by a projection of varying size called the styliform process. Finally, lateral to both of these openings is a much smaller and more irregular opening, the Glaserian (petrotympanic) fissure (Evans and Christensen, 1979: figs. 4–39), which in life permits the chorda tympani, as it exits the petrosal, to pass through the middle ear and into the infratemporal fossa. These openings between the bulla and the skull base can be difficult to illustrate as they tend to be deep within the ear region and may require an angled anterior approach to the temporal region to be seen. Another small basicranial opening is the craniopharyngeal canal, an unpaired midline passageway that runs through the body of the sphenoid from the sella turcica endocranially and through the basisphenoid ventrally. When patent in the adult, the canal creates a communication between the pharynx and the hypophyseal fossa that conducts small vessels and branches of the internal carotid nerve plexus (Arey, 1950). The descriptions below also include details of the bulla visible only when it is removed from the skull.

When the bulla is removed the relationship of the petrosal to surrounding bones becomes visible, and typically in the species described here, the petrosal has large, and even confluent, passageways on its anterior and medial sides. These passageways sometimes represent the union of several named foramina that are distinct in other mammals. Thus, in Artiodactyla the functional

passageway is preserved, but the integrity of the named foramen is not always maintained. I consider the homology in this case to be that the opening (foramen) is present and patent (as in O'Leary et al., 2013). There is precedent for this practice in other anatomical treatments including Kampen (1905) and in the illustrations of Sisson (1911) where openings such as the foramen ovale are identified in taxa for which this hole is not enclosed by a typical circumference of bone. Variation in these openings has also been described (Edinger and Kitts, 1954).

Moving around the promontorium of the petrosal counterclockwise from its anterolateral margin, the most lateral opening into the skull is the piriform fenestra (O'Leary et al., 2013: char. 564), which is positioned lateral to the anteriormost tip of the promontorium, known as the epitympanic wing (O'Leary et al., 2013: char. 579). Medial to the piriform fenestra is the carotid foramen (mentioned above), which may be referred to as the carotid incisure, but only if it is possible to discern a clear anterior notch in the basisphenoid. Continuing counterclockwise, the next most posterior opening is the middle lacerate foramen (O'Leary et al., 2013: char. 455) that is anteromedial/medial to the promontorium. This opening is followed by the basicapsular fissure (O'Leary et al., 2013: char. 569) more posteriorly and finally by the jugular foramen. Again, in some cases these foramina are confluent with each other, but nonetheless I apply the standardized terms to emphasize the underlying topological homology with other mammals. Anterior to all these foramina between the petrosal and the skull is the foramen ovale, which in Artiodactyla typically lies within the alisphenoid bone. The foramen ovale may also become confluent with adjacent foramina, in which case there may only be a notch within the alisphenoid or an incisura ovalis.

The bullae of Artiodactyla are often characterized by a sharp border at the ventralmost extreme and I refer to this as the bullar ridge. Additionally, in some ruminants in particular, the glenoid joint itself on the squamosal has two differently shaped parts: it is convex anteriorly and concave posteriorly. The anterior convexity I consider to be a preglenoid process following O'Leary et al. (2013). Also the term posttympanic process of the squamosal across mammals describes a ventral projection of bone (as applied in O'Leary et al., 2013). The term has, however, been used by Pearson (1927: fig. 1) to describe even a nonprojecting plate of bone that forms part of the fused complex at the external acoustic meatus of suids.

Institutional Abbreviations

AMNH-M	Department of Mammalogy, American Museum of Natural History, New York, New York
SBU-MAR	Department of Anatomical Sciences, Stony Brook University, New York
UCM-VZ	Museum of Vertebrate Zoology, University of California, Berkeley, California
UCR	University of California, Riverside
USNM-M	Division of Mammals, United States National Museum, Smithsonian Institution, Washington, D.C.

BASICRANIAL DESCRIPTIONS

Camelidae

Camelus dromedarius

Figures 2–4

The camelid skull has been described in the context of the gross anatomy of the species in a landmark study of the dromedary (Smuts and Bezuidenhout, 1987). *Lama guanicoe* has also been illustrated and described with several basic landmarks labeled (Starck, 1995), and variability in cranial openings has also been briefly discussed by Edinger and Kitts (1954). Descriptions

here are based on two adult specimens: SBU-MAR 31, which was illustrated after the removal of the auditory bulla (the petrosal in isolation from the same specimen, opposite side, was described by O'Leary, 2010), and AMNH-M 14111, which has the auditory bulla in situ. Descriptions of those two adult specimens were supplemented by information from subadult AMNH-M 6368.

The bones of the intact basicranium of *C. dromedarius* are highly fused; the auditory bulla and external acoustic meatus are tightly adhered (often without visible sutures) to the exoccipital, basioccipital, basisphenoid, alisphenoid, and squamosal (fig. 2). As noted above, the auditory bulla had to be sawed off SBU-MAR 31 to reveal the underlying petrosal in situ, the promontorium of which does not make direct contact with the underlying bulla.

Orbit and palate structures are not shown in the illustrations, nor are they preserved in the dissected specimen, however, some observations based on specimen AMNH-M 14111 are noted here. The relatively round sphenorbital fissure is much larger than, and is set posterior and ventral to, the optic foramen. The optic foramen is circular and has a prong of bone on its lateral border that extends several centimeters anteriorly. At the base of the sphenorbital fissure is a slit that is the anterior opening of the pterygoid canal. The pterygoid canal is short and straight such that a probe in this foramen emerges several centimeters through the posterior opening of the pterygoid canal at the posterior edge of the entopterygoid process in the roof of the basipharyngeal canal. In the specimen illustrated here, a long sulcus connects the posterior opening of the pterygoid canal to the anterior aspect of the middle ear region (figs. 2, 3).

Based on AMNH-M 14111, sutures on the palate are largely fused, making it possible to see only a weak indication of the suture where the pterygoid met the alisphenoid. In the roof of the basipharyngeal canal a large part of the vomer has extensive exposure posterior to the palate, obscuring the presphenoid-basisphenoid contact. The ento- and ectopterygoid processes are flanges that extend posteriorly and slightly laterally. The entopterygoid process with its hamulus has a much longer anteroposterior extent than does the ectopterygoid process and it is concave posteriorly. The pterygoid fossa is small and confined to the ventral one-third of the total height of the posterior wall of the basipharyngeal canal. The foramen ovale is a separate hole anterior to the middle ear region and is not confluent with any other adjacent skull-base openings (figs. 2, 3). It is situated entirely within the alisphenoid, but its lateral border lies very close to the suture with the squamosal. On its lateral side, the foramen ovale has a sharp crest that protrudes several millimeters ventrally and comes to a point anteriorly (fig. 3).

In the skull midline a craniopharyngeal canal is absent in the adults but present in the juvenile specimen. Only a hint of the suture between the basisphenoid and the basioccipital is visible in AMNH-M 14111, and it lies just anterior to the tympanic processes, which are situated entirely on the basioccipital (fig. 2). The tympanic processes are subtle structures represented only by roughened areas of bone set between the midline of the skull and the lateral edge of the basioccipital. There is no median crest in the midline of the basioccipital. The medial edges of the occipital condyles almost meet in the midline and there are flexion stops, each marked by a sharp ridge anteriorly, on the anterior aspects of the occipital condyles. The occipital condyles have a distinct occipital ridge dividing the ventral from the posterior surface of the condyle. The hypoglossal foramina lie in deep pits anterolateral to the flexion stops (figs. 2, 3). Bilateral accessory hypoglossal foramina lie anterior to the main hypoglossal foramina (fig. 2): in AMNH-M 14111 the accessory foramen opens into the foramen magnum; in SBU-MAR 13 it opens into the basicapsular fissure. The condyloid canal is absent upon inspection of the external aspect of the skulls, although I note that Smuts and Bezhuidenhout (1987) mention the presence of one in the roof of the hypoglossal canal. The paracondylar process of the

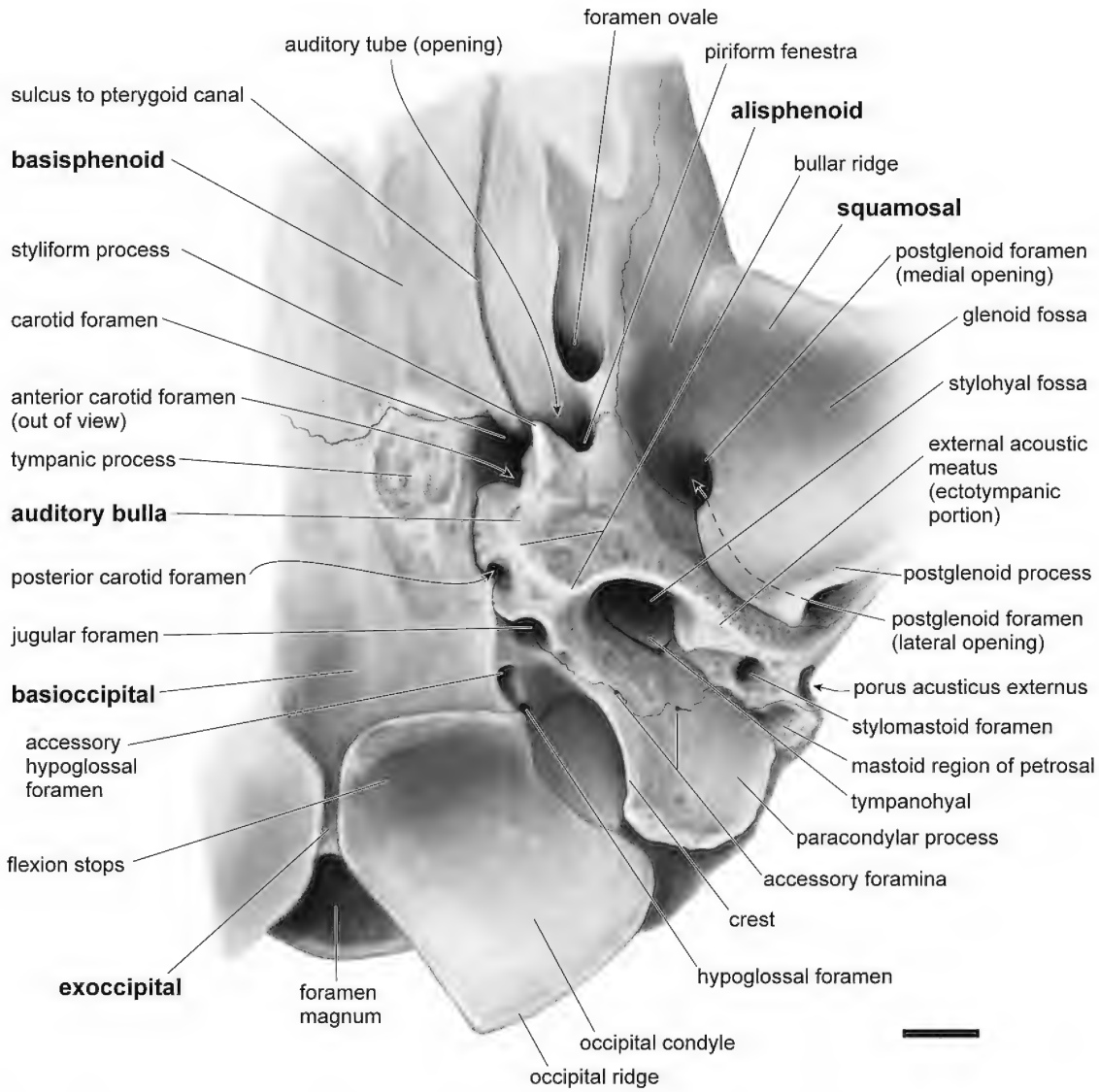

FIGURE 2. Left basicranium of *Camelus dromedarius* (Camelidae; AMNH 14111) with auditory bulla intact. Illustration was done prior to removal of bulla for illustration in figure 3. Scale bar = 1 cm. Artist: C. Lodge.

exoccipital is a curved ledge of bone that is concave posteromedially; its lateral margin is relatively straight. The paracondylar process has a roughened texture and extends to approximately the same distance ventrally as the bulla.

As noted above the auditory bulla is highly fused to surrounding bones. It consists of a tube-like external acoustic meatus that is approximately twice as long as the bulla is wide mediolaterally (figs. 2, 4). The external acoustic meatus has a rough surface ventrally. The porus acusticus externus is a small, circular, and laterally facing opening; it lies approximately at the same level as the middle ear (not significantly superior to it). The bulla has a roughened and complex surface, and in some specimens is pocked with many pin-sized foramina (fig. 2). The overall shape of the bulla is one of a very compressed ovoid with the long axis running anteromedial to posterolateral. A bullar ridge, an extensive crest running along

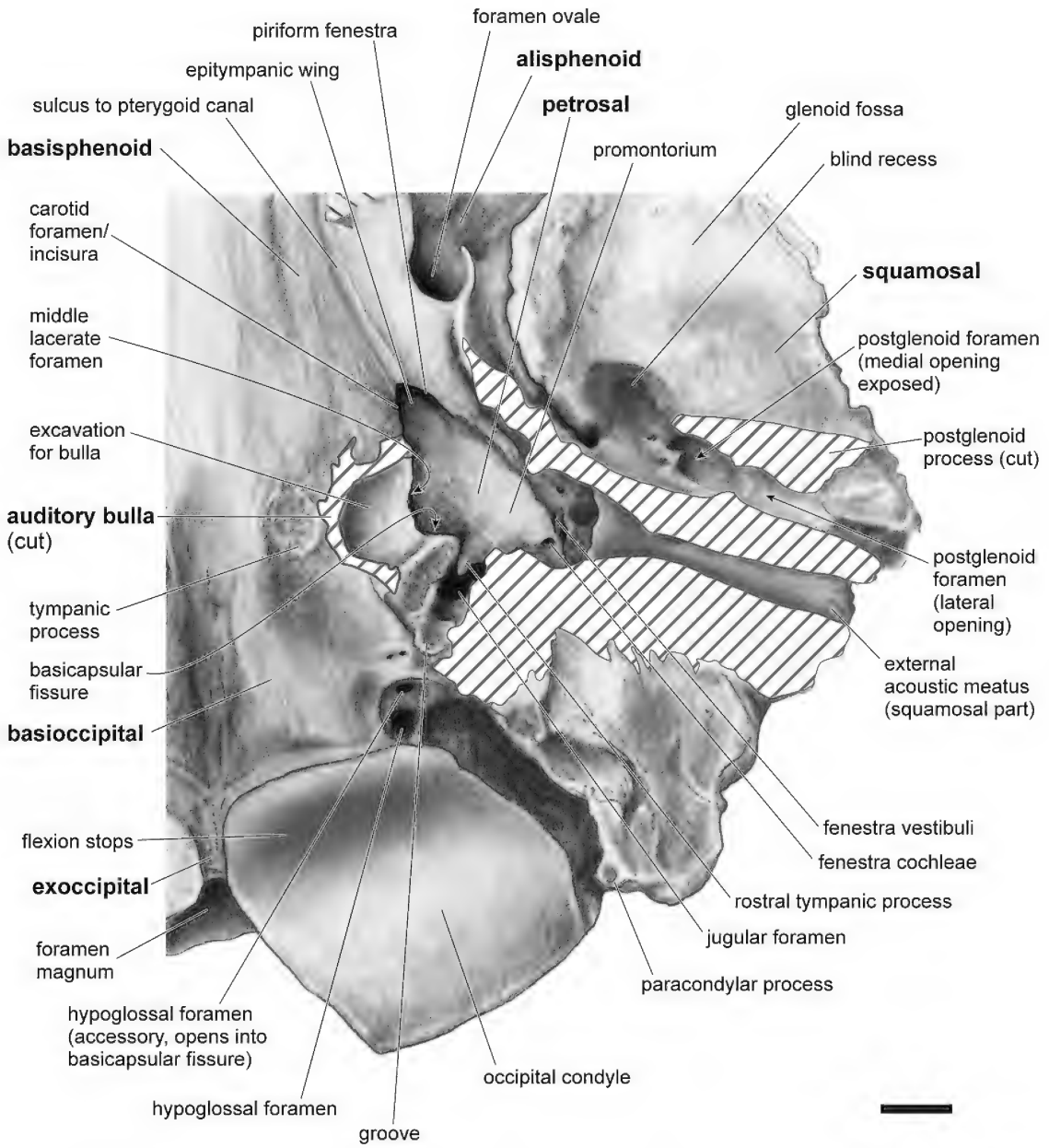

FIGURE 3. Left basicranium of *Camelus dromedarius* (Camelidae; SBU-MAR 31) with auditory bulla removed to reveal petrosal in situ. Scale bar = 1 cm. Artist: C. Lodge.

the ventral surface of the auditory bulla from anteromedial to posterolateral, marks this axis (fig. 2). The bullar ridge lies anterior to the stylohyal fossa and runs along the ventral surface of the external acoustic meatus. Running posteromedial to the stylohyal fossa, the bulla also has a separate prong of bone that fuses with the paracondylar process of the exoccipital (fig. 2). Two accessory foramina lie where the bulla meets the paracondylar process (fig. 2). Anteriorly the bulla has a very small styliform process that does not extend as far ventrally as other aspects of the

bulla, but does mark the position of the bony opening of the auditory tube.

With the bulla in situ it is difficult to view the piriform fenestra and the carotid foramen (discussed below). The anterior carotid foramen is set deeply on the anterior aspect of the bulla and lies adjacent to a sharp crest. Medially the bulla is in contact with, and partially fused to, the basioccipital, excavating it by way of a protrusion from the bulla (figs. 2–4). This configuration obscures a view of the basicapsular fissure and middle lacerate foramen while the bulla is in situ (fig. 2). This bullar contact with the basioccipital is a bulbous medial protrusion from the bulla (fig. 4) that leaves a smooth excavation in the basioccipital (fig. 3). Posterior to where the bulla abuts the basioccipital is the small and round posterior carotid foramen (called the fissura petrotympanooccipitalis in Smuts and Bezuidenhout, 1987: fig. 6). The posterior carotid foramen is partially separated from the larger jugular foramen by a crest of bone that juts posteromedially from the bulla. This crest does not fuse to midline bones. The large and round jugular foramen is clearly visible with the auditory bulla in situ (fig. 2). Smuts and Bezuidenhout (1987) described the jugular foramen as divided into medial and lateral parts. In AMNH-M 14111 there is essentially one opening, but it is partly divided by a small prong of bone that juts anteriorly from the exoccipital. The jugular foramen is very deep walled. It is not completely enclosed by the bulla as its posteromedial edge is formed by the exoccipital (fig. 2). Laterally, the tympanohyal is set deeply within the stylohyal fossa where it is tightly fused to the bulla anteriorly and the exoccipital posteriorly. The morphology of the subadult specimen suggests that the tympanic bulla encircles the tympanohyal completely. The tympanohyal has a flattened and broad ventral tip. Lateral to the tympanohyal is the stylomastoid foramen, a small round opening that is bordered by the exoccipital, the tympanic bulla, and the mastoid region of the petrosal, all of which are fused (fig. 2). There are no conspicuous grooves emanating from this foramen.

The bulla in isolation reveals a long and smooth internal surface to the external acoustic meatus, which makes an almost 90° bend along its course between the ectotympanic ring and the porus acusticus externus (fig. 4). With the bulla removed it is apparent that the anterior and medial parts of the pars cochlearis of the petrosal are very close to, but actually free of, contact with the surrounding alisphenoid, basisphenoid, and basioccipital bones (fig. 3). The petrosal is firmly held in place by sutures on its lateral and posterolateral sides. The petrosal overrides these other bony elements superiorly with several struts of bone extending across the basicapsular fissure without contacting midline structures. The mastoid region of the petrosal is somewhat obscured by fusion of the petrosal to the squamosal and exoccipital but is visible in ventral view. Figure 3 shows the elongate and straight squamosal contribution to the external acoustic meatus.

With the bulla removed (fig. 3) it is apparent that the piriform fenestra is an open, oval-shaped space that lies lateral to the pointed anterior extreme of the petrosal. The piriform fenestra is fully continuous with the carotid incisure/foramen, the latter being a larger, essentially oval opening close in size to that of the foramen ovale. The opening forms almost a complete circle by the approximation of the petrosal to the fused basisphenoid-alisphenoid, however, technically the pars cochlearis of the petrosal is not in contact with the midline bones (basisphenoid, basioccipital) and the carotid foramen is not closed. The basicapsular fissure is an irregular and elongate opening that connects the carotid incisure to the jugular foramen via a middle lacerate foramen winding between prongs of bone jutting from the midline and from the petrosal. The full extent of the jugular foramen does not differ greatly from that which was visible with the bulla in place. Forming the anteromedial border of the jugular foramen is a large and pointed rostral tympanic process that protrudes inferiorly from the petrosal. This process is most clearly visible in an isolated petrosal (O'Leary, 2010: fig: 33).

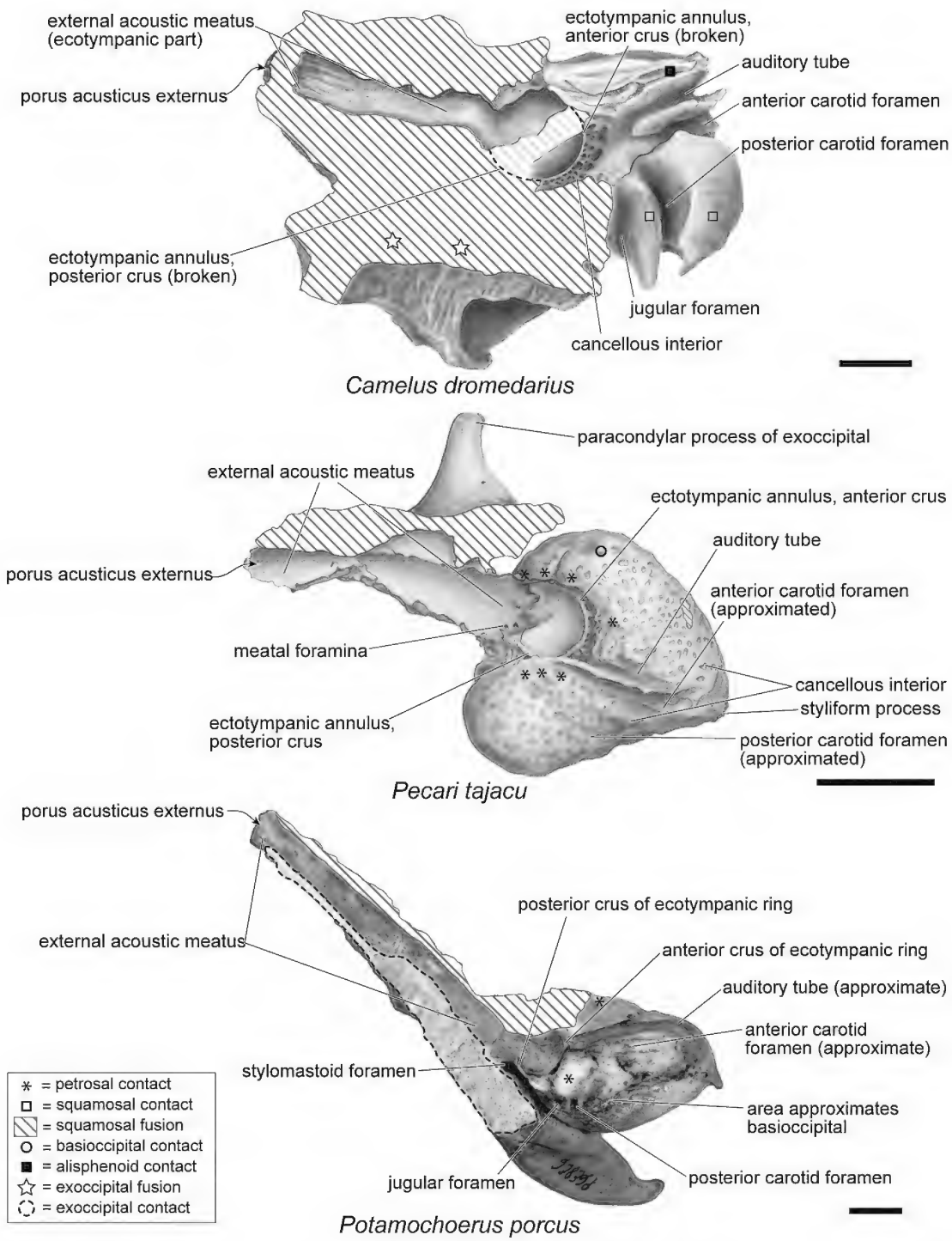

FIGURE 4. Left auditory bullae of *Camelus dromedarius* (Camelidae; SBU-MAR 31), *Pecari tajacu* (Suina; UCM-VZ 1247), and *Potamochoerus porcus* (Suina; AMNH-M 238329, reversed from right side) shown in dorsomedial view. Scale bar = 1 cm. Artists: L. Betti-Nash (*Camelus*), C. Lodge (*Pecari*); photograph: S. Goldberg.

The long axis of the glenoid fossa is oriented mediolaterally; the medial glenoid pit is absent (fig. 2). The fossa is relatively flat overall and oriented such that its posterior aspect is positioned more superiorly. The posterior aspect of the fossa is more concave directly anterior to the postglenoid process. The fossa has a small, inferiorly directed flange of bone at its most lateral extreme (out of view in the illustrations). The postglenoid process extends from the lateral edge to approximately the midpoint of the joint. It is a large lip of bone that is appressed to the anterior surface of the external acoustic meatus. The postglenoid foramen has openings on both the medial and lateral sides of the postglenoid process (figs. 2, 3). That these two postglenoid foramina are contiguous becomes apparent when the postglenoid process is removed, and it is the medial opening of the postglenoid foramen that leads into the endocranium. A blind recess lies lateral and adjacent to the medial opening of the postglenoid foramen (fig. 3). The posttympanic process of the squamosal is highly fused to the external acoustic meatus and does not extend much inferior to the external acoustic meatus, and certainly does not contact the postglenoid process. Due to its short extent, the posttympanic process is out of view in the illustrations.

Suina – Tayassuidae

Pecari tajacu and *Tayassu pecari*

Figures 4–6

Pearson (1927) described and illustrated key features of the ear regions of living and extinct Tayassuidae, particularly anatomical variation in proximity to the articulation of the mandible. Kampen (1905) provided details on the bulla, and Edinger and Kitts (1954) provided an illustration of tayassuid basicranial openings in the ear region. Descriptions and phylogenetic analysis of the petrosal in *Tayassu* and extinct relatives, including the relationship of the petrosal to surrounding cranial bones, have also been published by Orliac (2013).

The bulla is very tightly fused to surrounding bones in these species (e.g., adult specimen SBU-MAR 8), particularly the external acoustic meatus. In UCM-VZ 1247, a specimen of *Pecari tajacu,* the bulla was dissected off to expose the petrosal in situ. The larger species, *Tayassu pecari*, is represented by SBU-MAR 8. Both specimens are adults based on dental eruption, but UCM-VZ 1247 has a larger number of intact cranial sutures suggesting that it may have been ontogenetically younger than SBU-MAR 8 at death.

The optic foramen is distinctly circular. It is superomedial to the sphenorbital fissure and smaller than it. The sphenorbital fissure is oval in *Tayassu pecari* and more circular/irregular in *Pecari tajacu*; in each case the long axis of the fissure trends superomedial to inferolateral. No distinct anterior opening of the pterygoid canal is visible at the base of the sphenorbital fissure.

Both figures 5 and 6 show the posterior aspect of the basipharyngeal canal. The vomer terminates anterior to the posterior opening of the basipharyngeal canal, anterior to the suture between the presphenoid and the basisphenoid. The presphenoid forms the central and posterior part of the roof of the canal and terminates with a straight suture against the basisphenoid. The two pterygoids are visible on either side of the presphenoid and taper toward each other anteriorly, where they extend onto the bony palate. There is no conspicuous posterior opening for the pterygoid canal, and no conspicuous sulcus running anteriorly from the middle ear toward the pterygoid region. The hamulus is a small crest that flares laterally and is more pronounced in *Tayassu pecari* (fig. 5). The pterygoid fossa is shallow and flat with the ectopterygoid plate forming a particularly sharp posterior ridge.

The midline of the skull lacks a craniopharyngeal foramen. The suture between the basioccipital and the basisphenoid is preserved in *Pecari tajacu* but obliterated in *Tayassu pecari* (figs. 5, 6). The tympanic processes are irregular bumps on the lateral edge of the basioccipital. They do not contact the bulla and are separated from

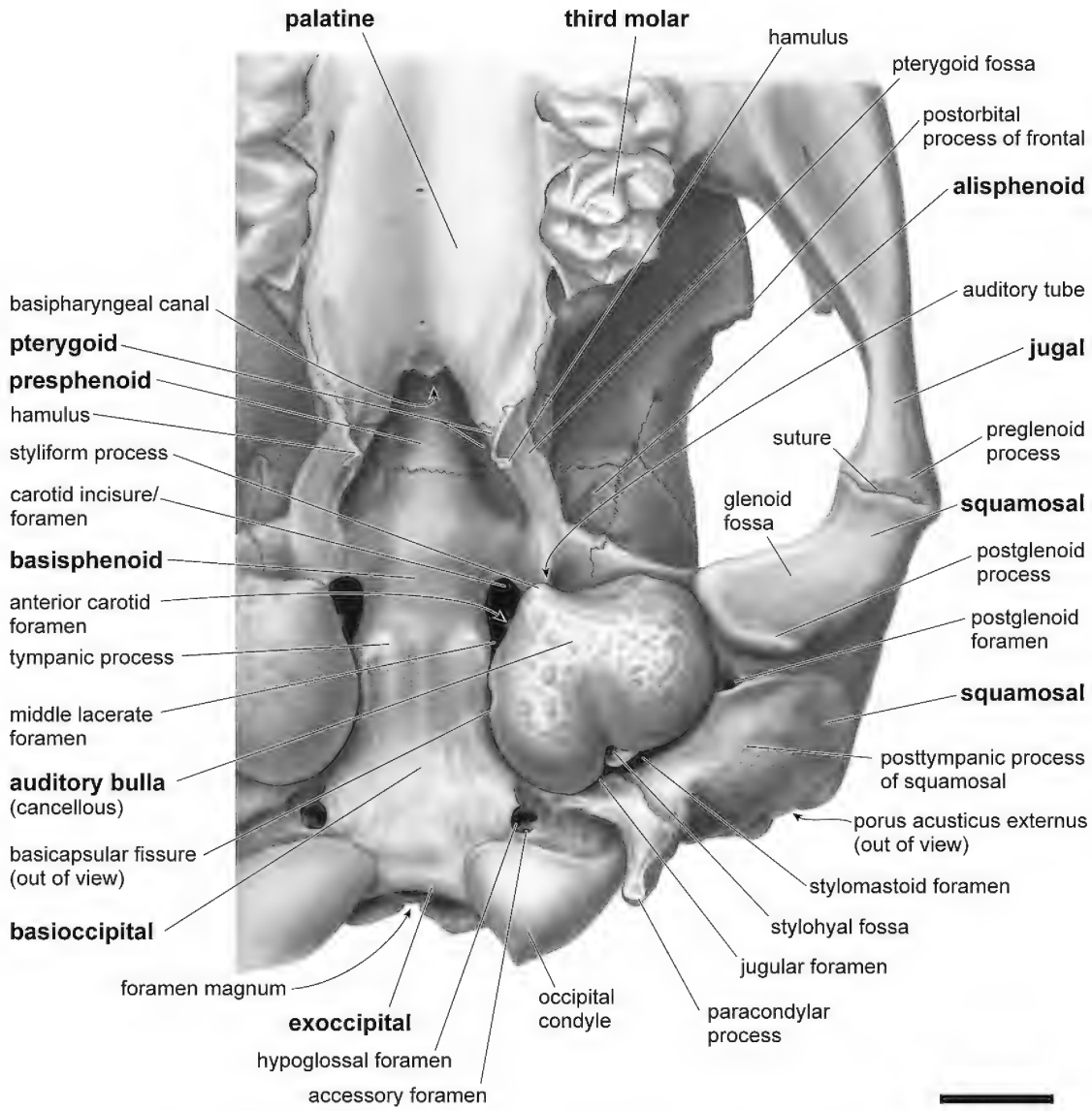

FIGURE 5. Left basicranium of *Tayassu pecari* (Suina; SBU-MAR 8) with bulla in situ. Scale bar = 1 cm. Artist: U. Kikutani.

each other by a midline crest. The occipital condyles are widely separated at their anterior margins and lack flexion stops. The condyles are divided into posterior and inferior surfaces that meet at a right angle. There is only a slight hint of an occipital ridge. Both specimens have hypoglossal foramina posteromedial to the jugular foramen that are distinctive in having one conspicuous external opening and a second smaller, accessory opening posterior to the hypoglossal foramen (fig. 6). These double foramina are inset into a larger, round depression and both open into the foramen magnum.

The bulla is bulbous and comes to a small styliform process at its anteromedial edge (fig. 5). As previously noted elsewhere (Kampen, 1905), the bulla does not protrude to a significant distance ventrally inferior to the glenoid fossa. The

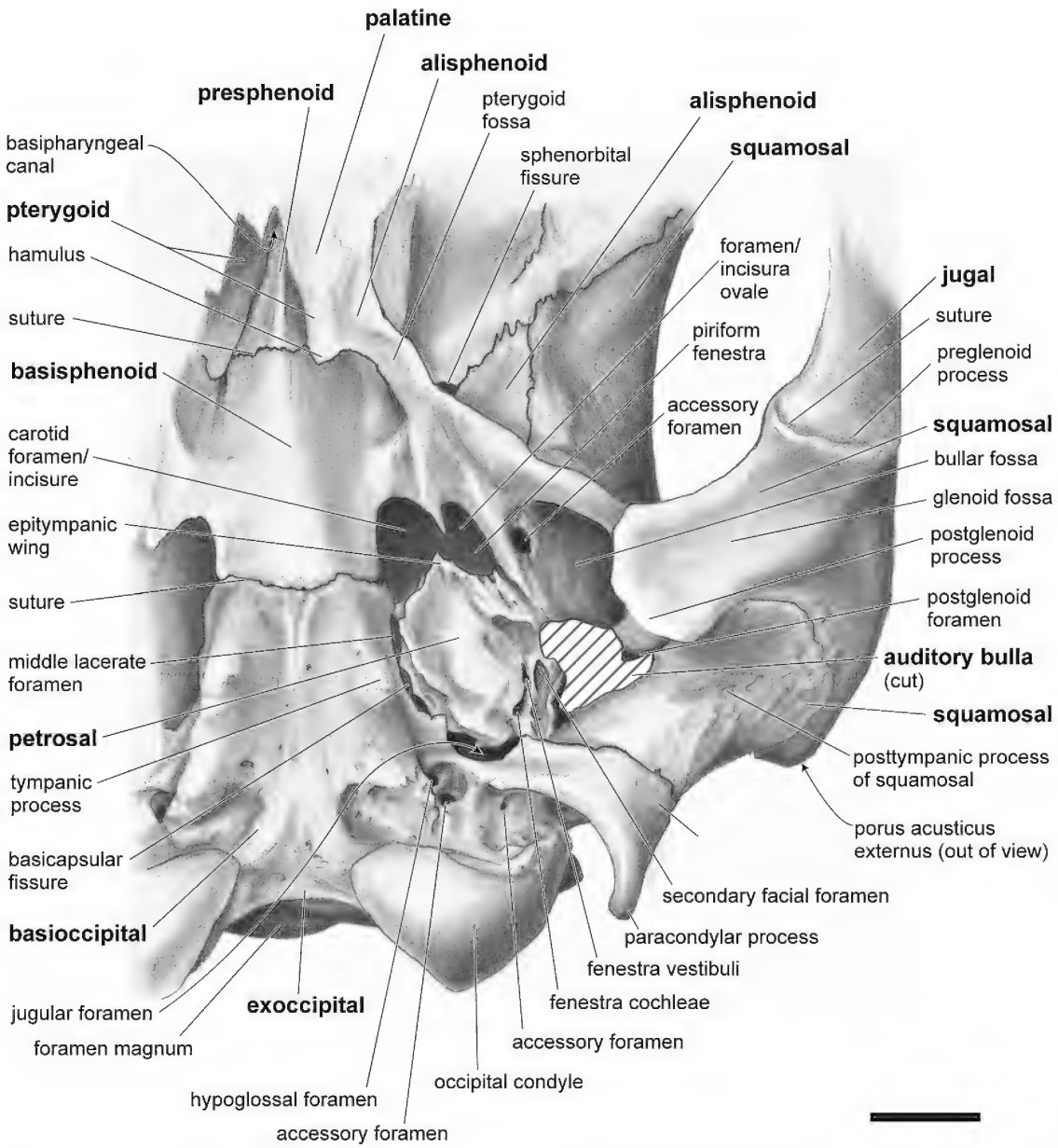

FIGURE 6. Left basicranium of *Pecari tajacu* (Suina; UCM-VZ 1247) with bulla removed to reveal petrosal in situ. Scale bar = 1 cm. Artist: C. Lodge.

external surface of the bulla is smooth. The bone is thin walled and nearly transparent exposing underlying trabecular structure throughout (figs. 4, 5). The bulla does not have a particularly pronounced bullar ridge marking the transition from its medial to lateral side. No tympanohyal is visible with the bulla in situ. If the tympanohyal is present, it is an extremely delicate and relatively small structure deeply recessed in the small, circular stylohyal fossa. In the subadult specimen of *T. pecari*, AMNH-M 133513, an independent tympanohyal is not apparent. The stylohyal fossa is completely enclosed within the posterior bullar wall and it is marked laterally by

a small crest from the bulla (fig. 5). The fossa extends anteriorly as a shallow groove on the bulla, dividing it into a larger lateral and smaller medial convexity. The stylomastoid foramen is lateral and slightly posterior to the stylohyal fossa. The exoccipital forms the posterior border of both the stylomastoid foramen and the medially adjacent jugular foramen.

The external acoustic meatus is a very long tube that is completely fused to the squamosal and exoccipital such that it is not apparent as a distinct structure in ventral view (fig. 5). There is a distinct suture posterior to the postglenoid process; in the adult it is not possible to determine whether this suture represents the complete fusion of the postglenoid and posttympanic processes of the squamosal around an the elongate external acoustic meatus, or whether some part of the external acoustic meatus remains exposed after fusion. Pearson (1927: fig. 1) described a "post-tympanic process" in *Pecari tajacu* and labeled it as the platelike portion of the squamosal located lateral and superior to the paracondylar process (= paroccipital process in Pearson's [1927: fig. 1] terminology). In mature specimens, however, this area does not conform to a shape that could be characterized as a process or projection that protrudes ventrally and is distinct from the ectotympanic, as is typical of a posttympanic processes (see examples illustrated across Mammalia in O'Leary et al., 2013: char. 555). The region in *Peccari* and *Tayassu* is instead a flat plate of bone that is highly fused. The mastoid region of the petrosal is also not visible on the external surface of the skull. The porus acusticus externus is out of view ventrally because it is situated posterior and distinctly superior to the bulla (fig. 5). Looking into the porus, a conspicuous circular scroll of bone can be seen. This scroll probably represents part of the ectotympanic, but the boundaries are difficult to discern due to its extensive fusion to the squamosal.

A very small paracondylar process projects from the exoccipital (figs. 5, 6). This process extends only a few centimeters inferior to the bulla itself in *Tayassu pecari*. In lateral view the paracondylar process is concave anteriorly and convex posteriorly. It has a slight flair at its ventral tip in *Tayassu pecari* but is a simple point that faces posteriorly in *Pecari tajacu*. At the base of the paracondylar process it is close to but not in contact with the auditory bulla.

With the exception of the anteromedial edge, the bulla is tightly appressed to the surrounding basioccipital, exoccipital, and squamosal. The carotid incisure/foramen and the incisura ovalis are, however, visible even with the bulla in situ (fig. 5). The anterior carotid foramen is a very deeply set structure, the entry to which is marked by a groove on the anterior bulla. When the bulla is in situ it is difficult to more than approximate the position of the posterior carotid foramen because it is so deeply set and it leaves no conspicuous marks on the bulla. With the bulla in situ, the jugular foramen is distinguished by a notch in the exoccipital (fig. 5). The basicapsular fissure is, however, not visible with the bulla in situ, because although the bulla is not fused to the midline, it is tightly appressed to the basisphenoid/basioccipital (fig. 5).

With the bulla removed it is apparent that the petrosal is held in place only on its lateral and posterolateral edges (fig. 6). It is not fused in place but wedged between the exoccipital and the squamosal where the small mastoid region is lodged. Anteriorly, the petrosal is not interdigitated into the surrounding bones. Thus, once the bulla is removed, the petrosal is also relatively easily removed, or, alternatively, the petrosal can be easily removed from the endocranial side of a bisected specimen with the bulla still in situ.

Figure 6 reveals the large, contiguous opening that separates the petrosal from the alisphenoid, basisphenoid, basioccipital, and, with the exception of a small strut of bone, also the exoccipital. The incisura ovalis is separated from the carotid incisure by a sharp prong of bone that does not reach the petrosal posteriorly. Laterally the incisura ovalis is fully open to the piriform fenestra. Adjacent to the piriform fenestra on the lateral side is a deep blind recess for the bulla. This recess contains an accessory foramen, not visible

with the bulla in situ, which opens into the endocranium. Posteromedial to the carotid incisure are the middle lacerate foramen and the basicapsular fissure. Each of these is a narrower opening than the carotid foramen/incisure. The basicapsular fissure is only partially separated from the jugular foramen by a small strut of bone from the exoccipital. This strut approximates but does not fully contact the petrosal. With the bulla removed it is apparent that the jugular foramen is more than double the size of what is visible when the bulla is in situ.

The glenoid fossa lies entirely on the zygomatic arch, primarily on the squamosal, and is aligned roughly with the ventral margin of the bulla (figs. 5, 6). A distinct, ridge-shaped preglenoid process is formed primarily by the jugal as it meets the squamosal. The glenoid fossa is concave with an oval outline with the long axis oriented from anterolateral to posteromedial. The postglenoid process is a narrow strut of bone that projects ventrally from the medial extreme of the joint to about the same distance inferiorly as does the preglenoid process. There is a single, small postglenoid foramen that is deeply set and lies directly posterior to the postglenoid process. The postglenoid foramen is visible whether the bulla is in situ or not. In *Tayassu pecari* this foramen is round and in *Pecari tajacu* it is more elongate and slitlike.

When removed and examined from its dorsomedial surface, the bulla has a relatively long, smooth external acoustic meatus that extends from the ectotympanic annulus (fig. 4). Presumably what is exposed internally is largely ectotympanic but, again, caution should be observed because the bones are highly fused to the squamosal and exoccipital. Several meatal foramina occur at the medial end of the external acoustic meatus. The ectotympanic annulus is a distinct semicircle for approximately 180° with no clear demarcation between anterior and posterior crura. Jutting from the annulus are several regularly spaced struts of bone that are contiguous with the more irregular cancellous structure otherwise present throughout the internal aspect of the bulla. As noted above, the auditory tube is marked by a distinct crest. The bulla had extensive contact with the petrosal and the squamosal (fig. 4).

Suina – Suidae

Potamochoerus porcus

Figures 4, 7, 8

Prior descriptions provided details of the cranial anatomy in a related member of Suidae, *Sus* (Parker, 1874; Sisson, 1911; Getty, 1975; Schaller, 1992), and Kampen (1905) also provided details regarding the auditory bulla of *Potamochoerus*.

Descriptions of the bulla in situ and removed are based on adult specimens AMNH-M 238330 and AMNH-M 53703, supplemented by AMNH-M 238329. Descriptions were also supplemented by examination of subadult specimen AMNH-M 100670. The lateral side of the bulla is firmly fused to the skull with the external acoustic meatus tightly sutured to the adjacent squamosal. In the adult, the petrosal in situ can be observed only with the bulla sawed off.

The optic foramen and sphenorbital fissure, which are out of view in the illustrations, are set very close together with the round optic foramen positioned slightly superior and anterior to the much larger and more oval sphenorbital fissure. About 3 cm anterior to the base of the sphenorbital fissure is a pin-sized hole that may be the anterior opening of the pterygoid canal but is too minute to probe for continuity with a posterior opening.

The surface of the palate is flat in a horizontal plane and ends in a small, superiorly directed posterior spine that receives contributions from the right and left palatine bones. There is no roughening or raised ridge where the two palatine bones meet at the midline suture. The ento- and ectopterygoid processes are platelike with sharp edges that are well separated ventrally, demarcating a distinct pterygoid fossa. The pterygoid fossa is deepest ventrally and flattens dorsally where it is defined only by crests on the

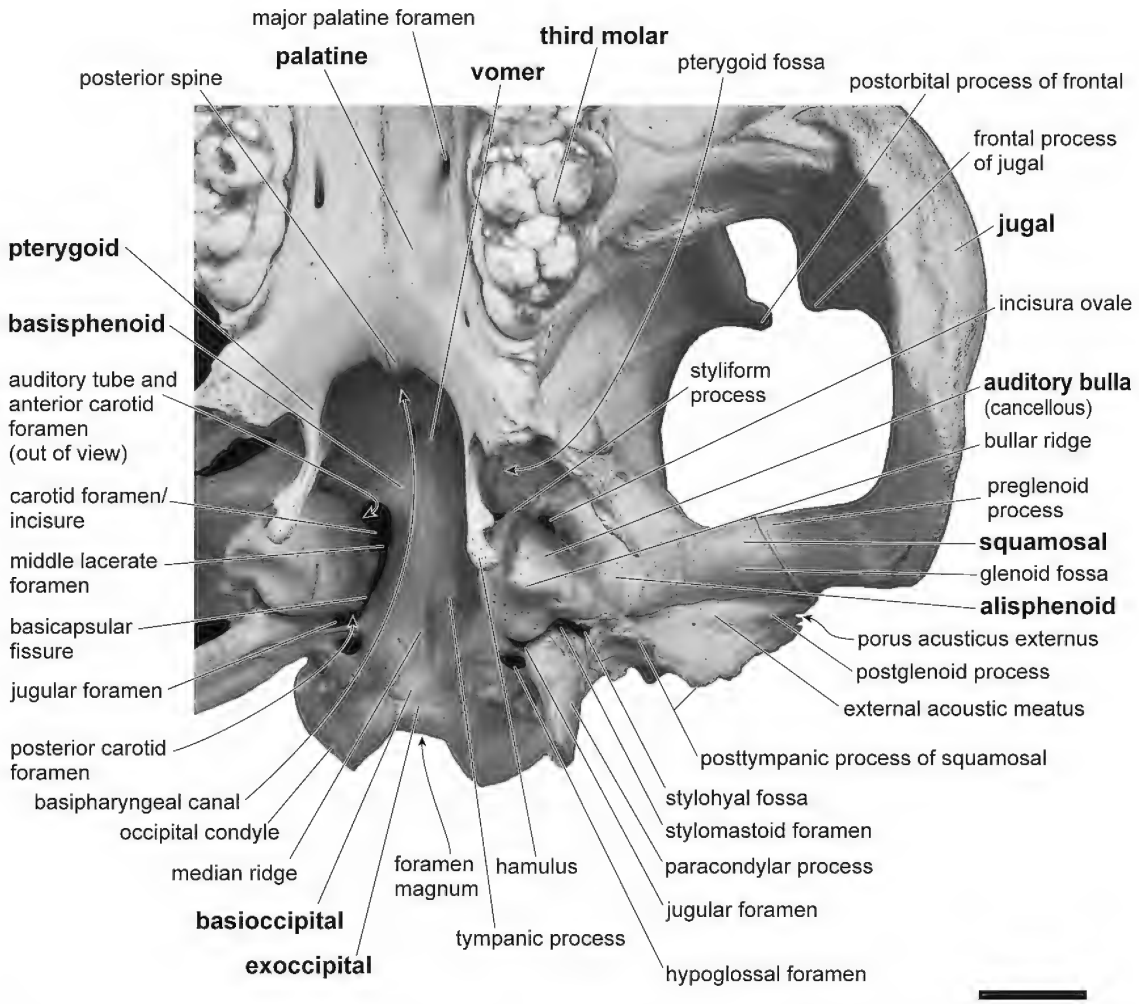

FIGURE 7. Basicranium of *Potamochoerus porcus* (Suina; AMNH-M 238330) with bulla in situ. Illustration is left side (image reversed from right side). Scale bar = 1 cm.

medial and lateral sides. Where the ecto- and entopterygoid processes meet ventrally, the palate surface is very roughened. The hamulus is a distinct prong extending posteriorly, ventrally, and slightly laterally from the rest of the entopterygoid process (figs. 7, 8). The hamulus terminates in a roughened knob.

In the roof of the basipharyngeal canal, the vomer, presphenoid, and pterygoid bones are visible (although the vomer sometimes covers the presphenoid entirely), however, the complete contours of each bone are hard to distinguish in the adult due to fusion with the basisphenoid and alisphenoid. The posterior end of the vomer lies just anterior to the presphenoid-basisphenoid suture and is apparent in AMNH-M 53703 (fig. 8). At the junction of the basisphenoid and the pterygoid is a pin-sized hole that is the posterior opening of the pterygoid canal. There is no particularly pronounced sulcus leading back from it to the middle ear. As noted above, the pterygoid canal is too narrow to easily establish continuity with a probe between its anterior and posterior openings.

The midline of the skull lacks a craniopharyngeal canal. A distinct median crest runs along the

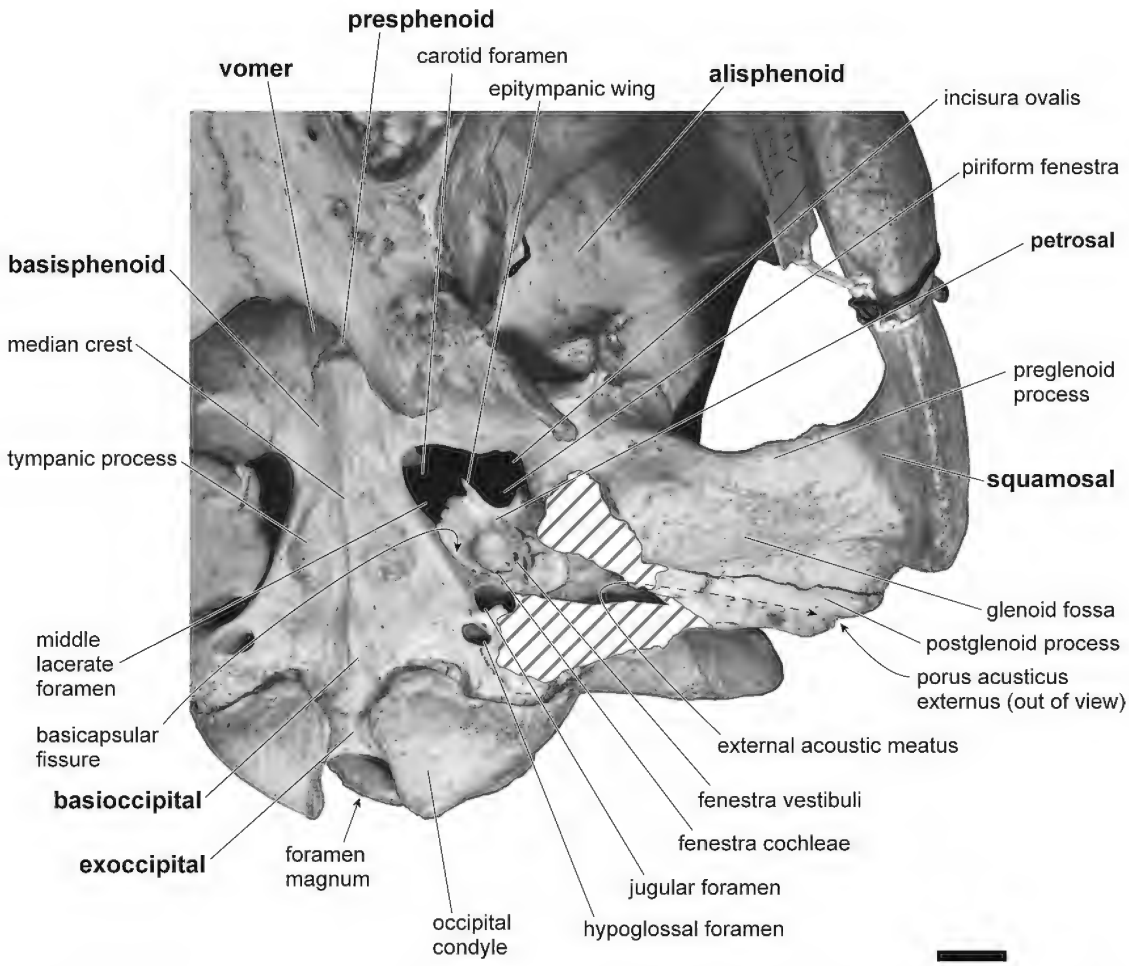

FIGURE 8. Left basicranium of *Potamochoerus porcus* (Suina; AMNH-M 53703) with bulla removed to reveal petrosal in situ. Photograph: S. Goldberg. Scale bar = 1 cm.

basisphenoid and basioccipital terminating just anterior to the occipital condyles. The tympanic processes are two small knobs positioned between the midline and the basicapsular fissure that have no contact with the bulla (fig. 8). The occipital condyles approximate each other in the midline but do not touch. They lack flexion stops and an occipital ridge, although the condyles do have distinct ventral and posterior planes. A single hypoglossal foramen opens into the anterior aspect of the foramen magnum (figs 7–8). The condyloid canal is absent. The paracondylar process is extremely long, extending well ventral to the bulla; it is oriented vertically and slightly anteriorly (fig. 7). It is of relatively uniform thickness from the base to the tip.

The bulla is ovoid, mediolaterally compressed and, as noted previously (Kampen, 1905), extends a good distance from the skull base with its longest dimension ventrodorsal (fig. 7). Its texture is smooth with pin-sized holes irregularly positioned on its surface. In ventral view a subtle bullar ridge that runs anteromedially to posterolaterally demarcates the ventralmost extreme of the bulla. At its inferiormost point the ridge forms a pointy bump that marks the ventral extreme of the bulla. A crest of bone is visible at the anteromedial margin of the bulla; this crest

is slightly scrolled and marks the medial side of the opening for the auditory tube.

The external acoustic meatus is extremely long relative to the mediolateral dimensions of the rest of the bulla, and wraps up the side of the skull such that the porus acusticus externus is substantially superior to the middle ear region (fig. 7). Distinctions between the postglenoid and posttympanic processes of the squamosal are difficult to discern because these processes are entirely fused to the elongate external acoustic meatus. Even in subadult specimens such as AMNH-M 100670, fusion of the squamosal and the ectotympanic is already largely complete: just a trace of a suture remains between the ectotympanic and the squamosal anterior to the external acoustic meatus, and no suture is visible between the squamosal and the ectotympanic posterior to the external acoustic meatus (the squamosal-exoccipital suture is clear in subadults). Using the subadult as a guide, one can estimate the positions of the sutures between the squamosal and the exoccipital and between the squamosal and the anterior aspect of the external acoustic meatus. The longest dimension of the glenoid fossa is mediolateral and the preglenoid process is just the ridgelike structure at the anterior part of the joint. The glenoid fossa is gently convex and lies in the same transverse plane as the skull base (fig. 7). The postglenoid foramen is absent. The postglenoid process is weakly developed in the adult and its identification is aided by comparison with subadult specimens. The postglenoid process is a small knob positioned at the lateral extreme of the joint.

A very long and pronounced crest extends from the bulla, and runs anterior to the stylomastoid foramen to the porus acusticus externus (fig. 7). The precise composition of the entire crest is unclear because of the obliteration of the squamosal-ecotympanic suture, but the posterior face of the crest almost certainly consists of squamosal, consistent with descriptions by Pearson (1927). This crest is the posttympanic process. The squamosal also contributes a small amount of bone to the anterior aspect of the base of the paracondylar process (as noted by Pearson, 1927).

At the anteromedial edge of the bulla there is no significant formation of a styliform process (fig. 7). Passageways into the bulla in this area, such as the anterior carotid foramen and the opening for the auditory tube, are very deeply set and completely out of view when the bulla is in situ. The carotid incisure is a large opening that is visible even when the bulla is in situ. It is fully continuous with the basicapsular fissure. Posterior to the basicapsular fissure the basioccipital widens and almost contacts the bulla. This configuration partially separates the jugular foramen from the basicapsular fissure when the bulla is in situ. When the bulla is in place the jugular foramen is oval and small and is positioned directly anterior to the hypoglossal foramen. The bulla forms the anterior border of the jugular foramen; the medial and posterior borders are formed by the fused exoccipital/basioccipital. Lateral to the jugular foramen the paracondylar process abuts the bulla closely but does not fuse to it. This arrangement fully separates the small, round stylomastoid foramen from the jugular foramen. Anterior to the stylomastoid foramen is a sharp crest of bone on the posterior bulla, which, as noted above, is contiguous with the posttympanic process of the squamosal. There is no distinct channel for cranial nerve VII external to the stylomastoid foramen. The stylohyal fossa is deep and vertically oriented and does not contain a visible tympanohyal.

With the bulla removed, the extent of the opening between the petrosal and the surrounding alisphenoid and basisphenoid is apparent (fig. 8). The piriform fenestra, incisura ovalis, carotid foramen, middle lacerate foramen, and basicapsular fissure all form a single, very large opening. Between the basicapsular fissure and the jugular foramen, however, the basioccipital and the petrosal approximate each other forming a partial separation between these two openings (however, technically the

basioccipital and the petrosal do not touch). With the bulla removed it becomes apparent that the jugular foramen is large and irregularly shaped.

As noted above, the bulla is completely sutured to the skull, and the squamosal and the exoccipital have to be sawed to expose an in situ petrosal. AMNH-M 53730 does not have the bulla preserved, so descriptions are made from AMNH-M 238329, which is a disarticulated skull.

The bulla has extensive contacts with the petrosal in an irregular pattern around the ectotympanic ring (fig. 4). The bulla does not fuse with the petrosal. In complementary fashion, looking at the petrosal (O'Leary, 2010; fig. 4), it is on the epitympanic wing and the flanges surrounding the promontorium where the bullar contact occurs. The bulla also has a large convex process (visible with bulla in situ) that abuts the basioccipital. When the bulla is removed and examined from its dorsomedial surface, the relatively long, smooth external acoustic meatus is visible as it extends from the ectotympanic annulus. The porus acusticus externus is irregular and jagged. Meatal foramina are not conspicuous on the inside of the external acoustic meatus but may be very minute. The tympanic annulus is a distinct semicircle for approximately 180° with no clear demarcation between anterior and posterior crura. Jutting from the annulus are several regularly spaced struts of bone that are contiguous with the cancellous internal structure of the bulla. The bulla is cancellous throughout and is made up of bone that is so thick that when viewed externally the cancellous bone beneath is obscured. Extending toward the nasopharynx is a pronounced channel that forms the bullar contribution to the auditory tube. A sharp ridge delineates it. The anterior carotid foramen is not very distinctive and may have been contiguous with this or closely adjacent to it. The bullar contributions to the posterior carotid foramen and the jugular foramen are marked by a pair of subtle grooves (figs. 4, 7).

Babyrousa babyrussa

Figures 9–11

Prior descriptions provided details of the cranial anatomy in a related member of Suidae, *Sus* (Parker, 1874; Sisson, 1911; Getty, 1975; Schaller, 1992), and Kampen (1905) provided details of the auditory bulla of *Babyrousa*.

The basicranium is described from two specimens: AMNH-M 152858, with the bulla in situ, and AMNH-M 2238, in which the bulla has been sawed off to expose the petrosal. I also consulted AMNH-M 152861, a subadult, to examine sutures, which are typically fused in adults. In the adult, the petrosal is not visible with the bulla in situ.

The sphenorbital fissure is oval with the long axis directed superior to inferior. It is inferolateral to the circular opening for the optic canal (fig. 10). The vomer is visible in the basipharyngeal canal; it has a very fragile and thin posterior edge that terminates in an irregular edge (figs. 9, 10). The hard palate is smooth and its posterior edge is inflected superiorly; a sharp ridge denotes the suture of the right and left palatines (fig. 9). Each palatine bone contributes to part of the posterior spine in the midline and the suture between the two palatine bones is visible. The much larger, single major palatine foramen lies just anterior to the third molar, and as many as three, more irregularly shaped, and much smaller minor palatine foramina lie posterior to it, closely adjacent to the third molar. The hamulus of the pterygoid is a mediolaterally compressed plate that terminates in a pointed, superiorly directed hook (fig. 9).

The longest dimension of the glenoid fossa is mediolateral, and the fossa is in the same transverse plane as the skull base, in other words, substantially superior to the inferior margin of the bulla (fig. 9). The fossa is gently convex and continuous with a preglenoid process anteriorly. There is a small medial glenoid pit. The postglenoid process of the squamosal is at the lateral edge of the glenoid fossa where it forms a small bump. The postglenoid foramen is absent.

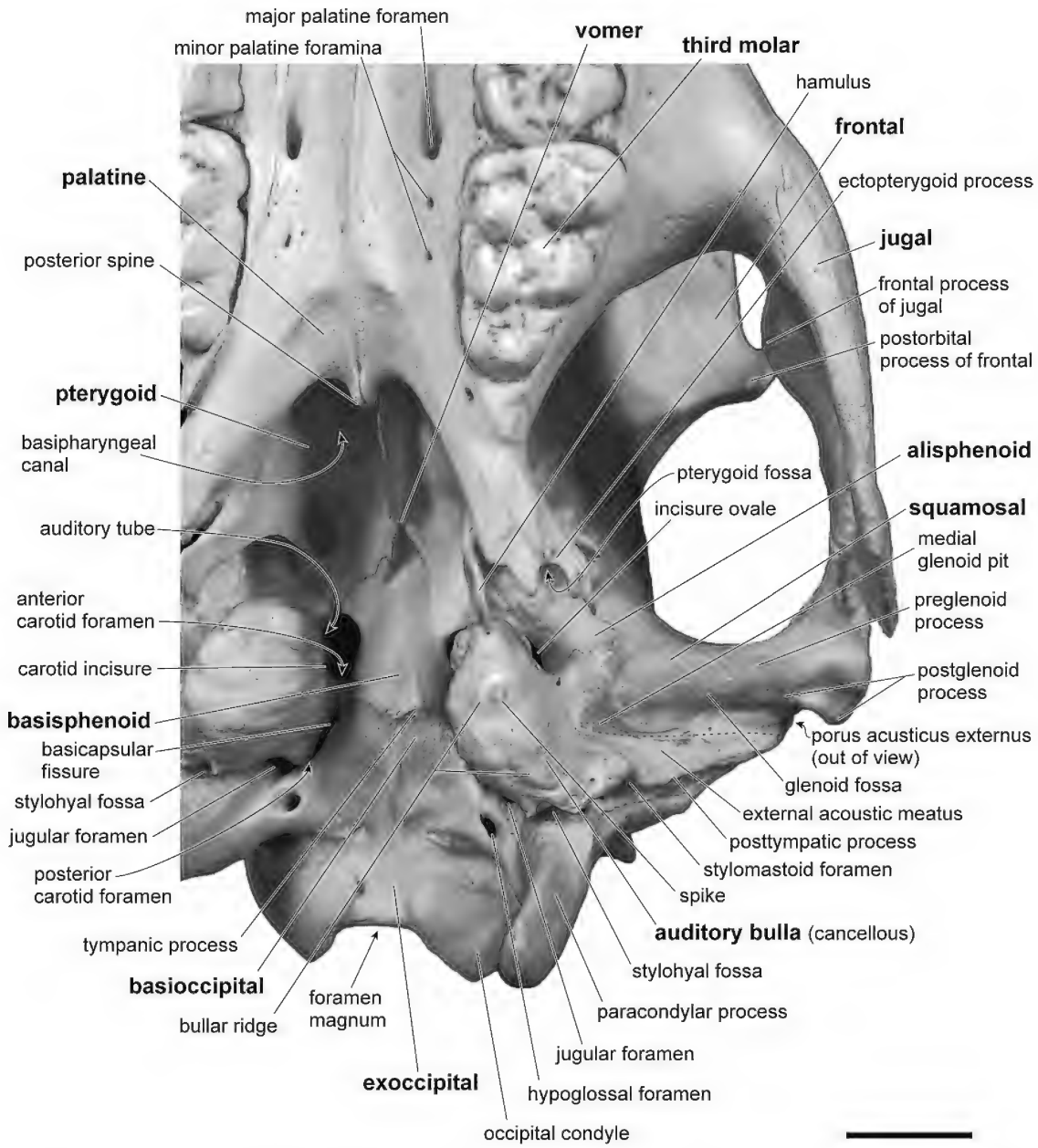

FIGURE 9. Basicranium of *Babyrousa babyrussa* (Suina; AMNH-M 152858) with bulla in situ. Scale bar = 1 cm.

Sutures between the squamosal and the ectotympanic are almost entirely obliterated in the adult specimen and even in subadults (fig. 9). The suture between the exoccipital and the squamosal is clear and the squamosal contributes a small amount of bone to the anterior base of the paracondylar process. Figure 9 shows an estimate of the position of the anterior suture between the squamosal and the ectotympanic, the latter forming a very elongate external acoustic meatus. Posterior to the external acoustic meatus, a sharp and distinct ridge ascends from the bulla, runs anterior to the stylomastoid foramen and terminates at the inferior margin of the porus acusti-

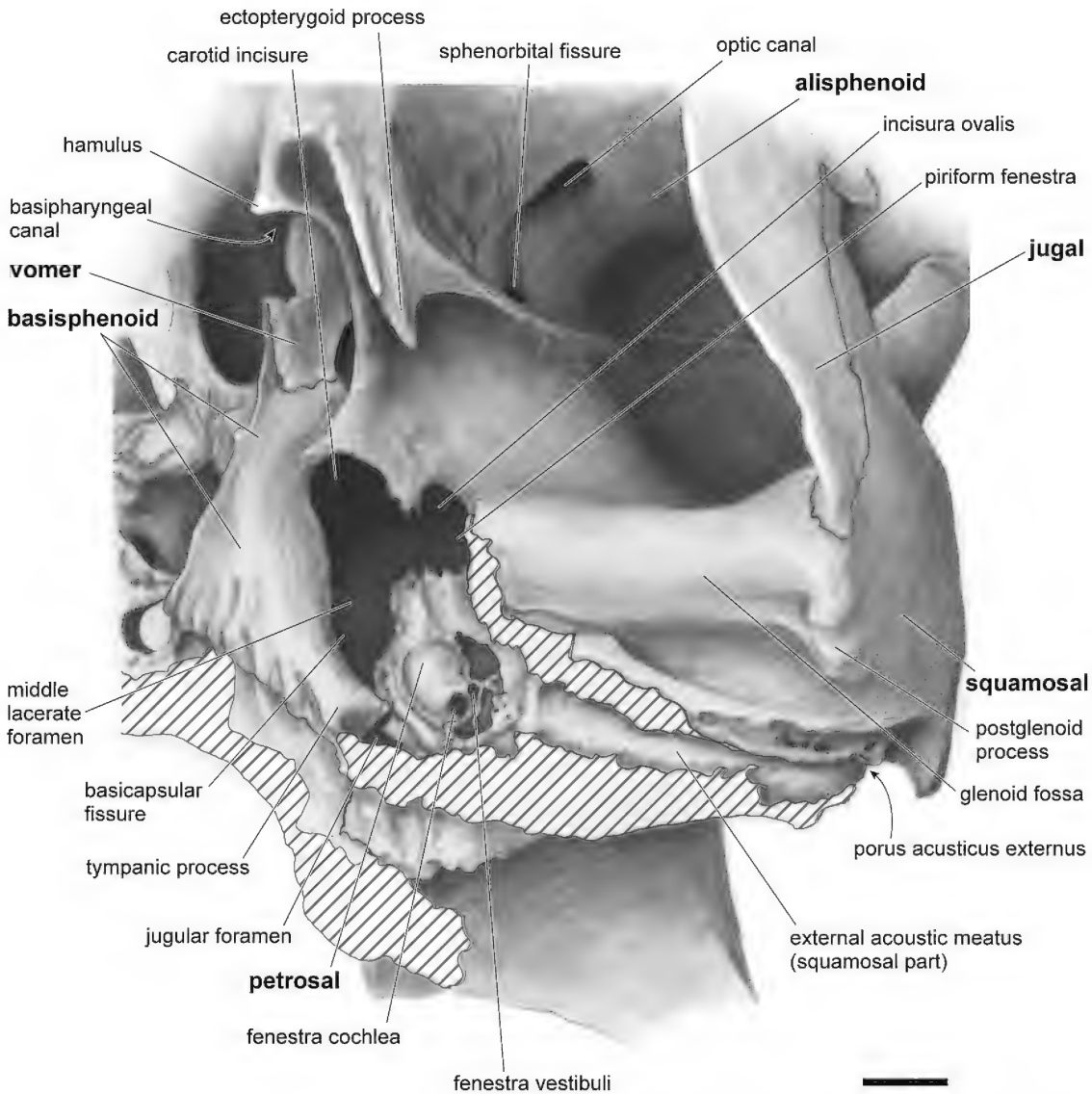

FIGURE 10. Basicranium of *Babyrousa babyrussa* (Suina; AMNH-M 2238) with bulla removed to reveal petrosal in situ. Scale bar = 1 cm. Artist: C. Lodge.

cus externus. This is the posttympanic process of the squamosal (following the general descriptions of Pearson, 1927), although it is somewhat ambiguous where the ectotympanic ends and the squamosal begins. The porus acusticus externus is substantially superior to the middle ear region.

In the midline the craniopharyngeal canal is absent. A roughened ridge indicates where the basioccipital meets the basisphenoid. The tympanic processes are not prominent structures and are distinctly separate from the auditory bulla (fig. 9). The occipital condyles are not in contact. They have distinct ventral and posterior surfaces but lack a pronounced ridge separating these surfaces. There is a single, distinct hypoglossal foramen that opens widely into the foramen magnum.

The paracondylar process of the exoccipital is blunt tipped and uniform in shape over its entire

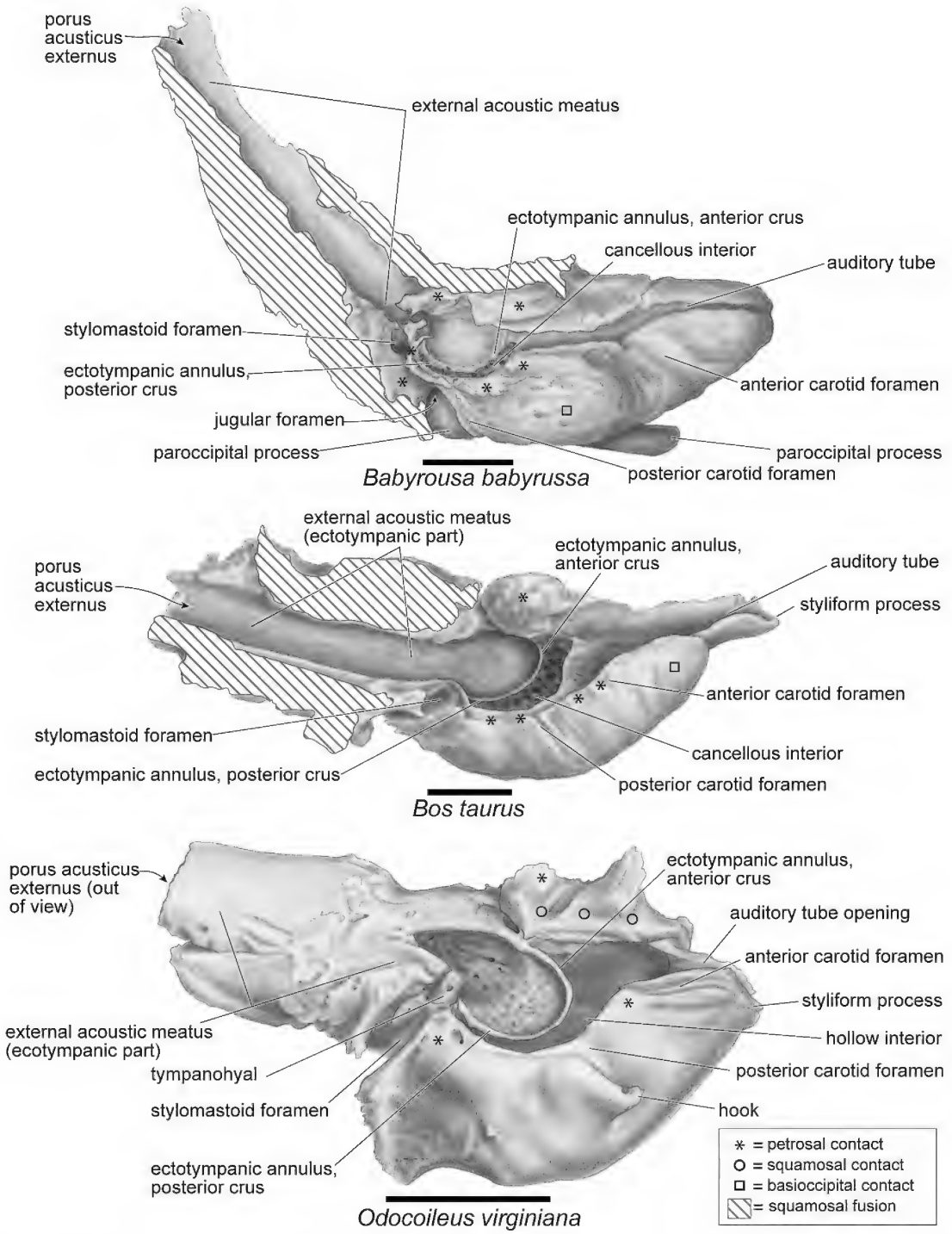

FIGURE 11. Left auditory bullae of *Babyrousa babyrussa* (Suina; AMNH-M 2238), *Bos taurus* (Cetruminantia, Ruminantia, Bovidae; SBU-MAR 14), and *Odocoileus virginianus* (Cetruminantia, Ruminantia, Cervidae; SBU-MAR 20), shown in dorsomedial view. Scale bar = 1 cm. Artists: C. Lodge (*Babyrousa*), L. Betti-Nash (*Bos*), and U. Kikutani (*Odocoileus*).

length. In lateral view, this process extends well below the auditory bulla. At its superior aspect, the process has an abrupt bend as it descends from the skull base; below the bend it straightens and is angled anteriorly. At its superior end it is in close approximation to the auditory bulla but not in contact with it. When the bulla is in situ its distinct bullar ridge can be palpated and, coming off the ridge at its most inferior position, is a small pointy spike (fig. 9). The overall shape of the bulla is ovoid with a roughened surface. The bulla is mediolaterally narrow and extends ventrally well below the level of the glenoid fossa, as previously noted (Kampen, 1905). The stylohyal fossa that invaginates the posterolateral edge of the bulla is defined on both its medial and lateral sides by ridges on the bulla (fig. 9). A tympanohyal is not visible in the stylohyal fossa. The ridge on the lateral aspect of the stylohyal fossa forms the medial aspect of the stylomastoid foramen. There is a groove external to the stylomastoid foramen running along the posttympanic process of the squamosal. Via fusion to the posttympanic process of the squamosal, the bulla is completely sutured to the skull anterior to the exoccipital and has to be sawed off to expose an in situ petrosal or the bulla's dorsomedial side. The bulla does not, however, fuse with the petrosal.

The carotid incisure and the incisura ovalis are visible in the space between the bulla and midline bones, even when the bulla is in situ (fig. 9). Anteriorly the opening of the auditory tube is inconspicuous in ventral view as it is tucked deeply into the skull base. The anterior carotid foramen does not leave a conspicuous mark on the bulla (fig. 11). The bullar contribution to the posterior carotid foramen is marked by a subtle groove just anterior to the bullar contribution to the jugular foramen. The bulla forms the anterior border of the jugular foramen, with the medial and posterior borders formed by the exoccipital (fig. 9).

With the bulla removed it is apparent that there is extensive space between the petrosal and the surrounding bones anterior and medial to it (fig. 10). Most laterally, the piriform fenestra is poorly defined and blends entirely with the incisura ovalis. The incisura ovalis is separated from the carotid incisure by a small, posteriorly directed prong of bone extending off what is probably the alisphenoid (sutures are fused). The carotid incisure is very large and wide, making a deep notch in the basisphenoid. This opening blends fully with the middle lacerate foramen and the basicapsular fissure, which is less clearly defined but is still a broad space between the petrosal and basisphenoid-basioccipital in the midline. The jugular foramen is the most separated of these skull-base openings and is defined by a prong of bone from the basioccipital that almost meets the petrosal (fig. 10). The squamosal part of the external acoustic meatus is smooth and wraps onto the lateral surface of the skull.

When the bulla is removed and examined from its dorsomedial surface, the relatively long, smooth external acoustic meatus is visible as it extends from the ectotympanic annulus (fig. 11). The bulla has extensive contacts with the petrosal in the vicinity of the ectotympanic annulus. As noted above, the bulla does not, however, fuse with the petrosal. In complementary fashion, it is on the flanges of the petrosal surrounding the bulging promontorium where in life the bulla contacts from below (see also O'Leary, 2010). The bulla also has a large convex process that abuts the basioccipital but does not fuse, or in some specimens (e.g., AMNH-M 152858) the bulla and basioccipital are very closely adjacent but not in contact. The ectotympanic part of the porus acusticus externus is irregular and jagged. Meatal foramina are not conspicuous on the inside of the external acoustic meatus. The ectoympanic annulus is a distinct semicircle for approximately 180° with no clear demarcation between anterior and posterior crura. Two irregular prongs of bone extend from the annulus and almost extend it to make a complete circle. Jutting from the annulus are several irregularly spaced struts of bone that are contiguous with the cancellous structure of the bulla. The bulla is cancellous throughout and its external bony surface is thin enough that the cancellous internal structure is visible through the bone in strong

light. In the region of the ectotympanic, the edge of the bulla curves inward near where it makes contact with the petrosal. Extending from this curvature, a pronounced channel forms the canal for the auditory tube, and runs the length of the bulla. It is delineated by a sharp ridge. Markings on the dorsomedial surface of the bulla for the anterior and posterior carotid foramina are subtle channels.

Cetruminantia – Ruminantia – Pecora – Bovidae

Bos taurus

Figures 11–13

There are several sources on *Bos taurus* basicranial anatomy (Sisson, 1911; Getty, 1975; Schaller, 1992), but in some cases the terminology differs from that used in contemporary comparative anatomy and paleontology works (Wible, 2003; Giannini et al., 2006; O'Leary et al., 2013) and many key structures are not labeled. The description here is based on two adult specimens: the bulla in situ is based on SBU-MAR 15 (fig. 12), and the bulla removed is based on SBU-MAR 14.

Several orbit landmarks are visible in figure 13. The optic foramen is round and the sphenorbital fissure is oval to teardrop shaped with a broad base inferiorly. The anterior opening of the pterygoid canal is a small slit at the base of the sphenorbital fissure; continuity with the posterior opening in the basipharyngeal canal is easily established with a probe. The foramen ovale is entirely contained within the alisphenoid directly anterior to the styliform process of the bulla.

Figure 12 shows the posterior aspect of the basipharyngeal canal. The vomer extends far enough posteriorly that it is broadly visible as a significant component of the basipharyngeal canal roof. It terminates just anterior to the suture between the presphenoid and the basisphenoid. The pterygoid bones extend slightly distal to the posterior edge of the vomer and form important elements of the lateral wall of the basipharygneal canal and a small component of the orbital wall. The posterior edge of the basipharyngeal canal is a complex arrangement of the pterygoid, alisphenoid, and palatine. Anteriorly the palatine alone forms the ventral margin of the basipharygneal canal, but posteriorly the pterygoid also extends to contribute to the ventral edge of the canal. The alisphenoid is less extensive and is primarily limited to the lateral wall of the basipharyngeal canal. The hamulus is a very diminutive hook that projects posteriorly and laterally. There is no pterygoid fossa and no significant development of entopterygoid processes. At the posterior end of the pterygoid bones on the superior aspect of the basipharygneal canal is a small but distinct posterior opening of the pterygoid canal.

A craniopharyngeal canal lies between the anterior aspects of the tympanic processes in the midline (fig. 12). The tympanic processes are pronounced, roughened, and oval knobs. They are positioned anterior and medial to the bulla and have no contact with it. The anterior ends of the occipital condyles are distinctly separate anteriorly. They have pronounced flexion stops (fig. 12). The occipital condyles have distinct ventral and posterior surfaces separated by an occipital ridge. The paracondylar processes are short projections that are angled slightly toward the midline as they descend. They extend inferior to the ventral edges of the bulla and its styliform process. They terminate in a subtle knob. A large, single hypoglossal foramen is present on each side tucked superior to the flexion stops (there is one accessory hypoglossal foramen on the left side in SBU-MAR 15; fig. 12). This hole is wide, giving very direct passage between the foramen magnum and the outside of the skull. By contrast, the two condyloid canals, which are smaller than the hypoglossal foramina and posterolateral to them, have a longer route through the exoccipital between the foramen magnum and the outside of the skull.

The auditory bulla is relatively tightly held in place, particularly posteriorly and laterally (fig. 12). In the adult, the petrosal is almost fully obscured when the bulla is in situ. The bulla has

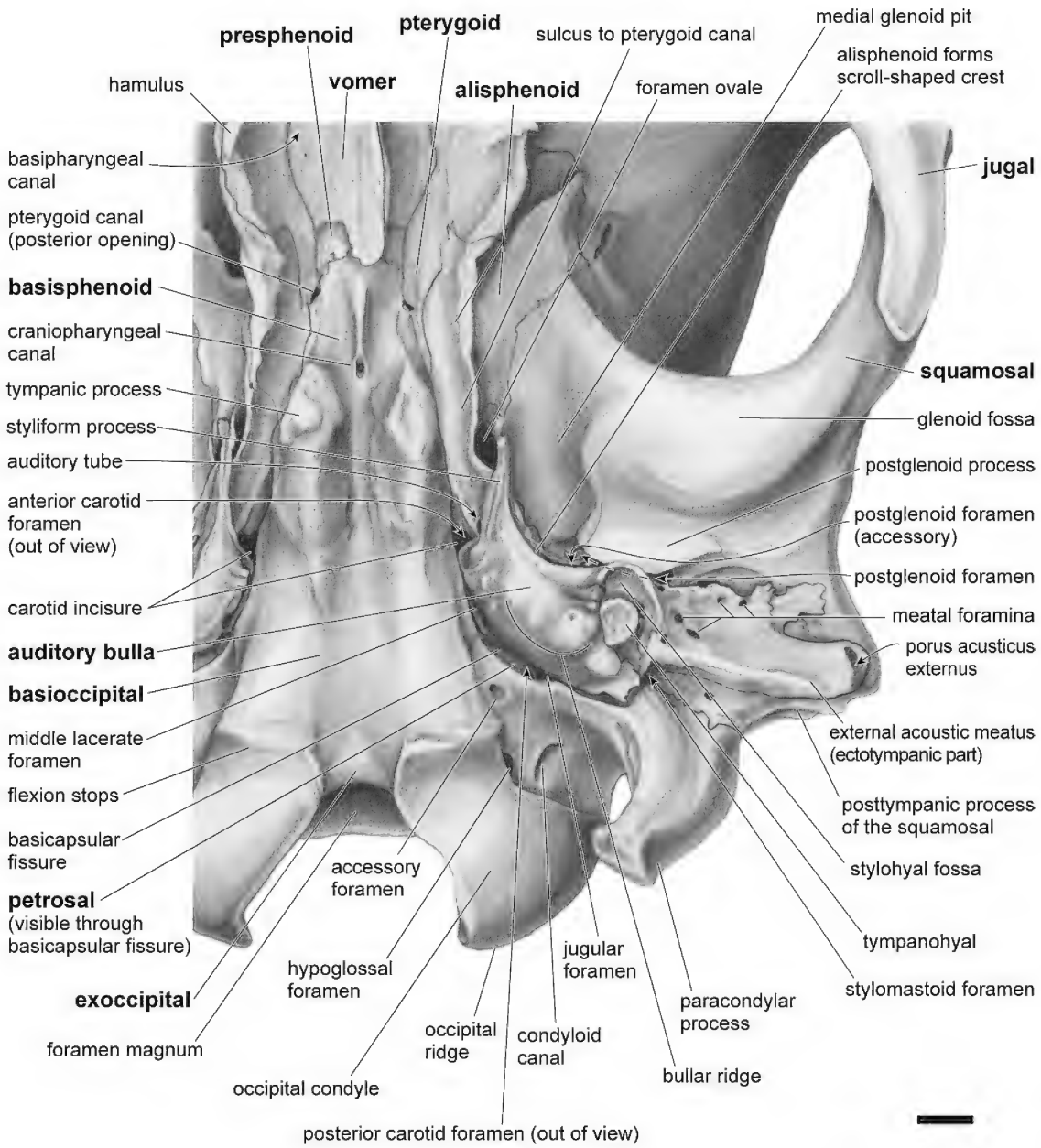

FIGURE 12. Left basicranium of *Bos taurus* (Cetruminantia, Ruminantia, Bovidae; SBU-MAR 15) with auditory bulla in situ. Scale bar = 1 cm. Artist: C. Lodge.

a compressed, elongate ovoid shape that is oriented along an anteromedial to posterolateral axis. The bone is smooth textured and in places (e.g., posteromedially), so thin as to be transparent, revealing its internal cancellous structure through the bone. At the anteromedial extreme is a pronounced styliform process—a thin, elongate spike with a significant anteroventral projection that extends well inferior to the basisphenoid. The long styliform processes are widest at their bases where they contact the auditory bulla (figs. 11, 12). The ventral edge of the bulla bears a

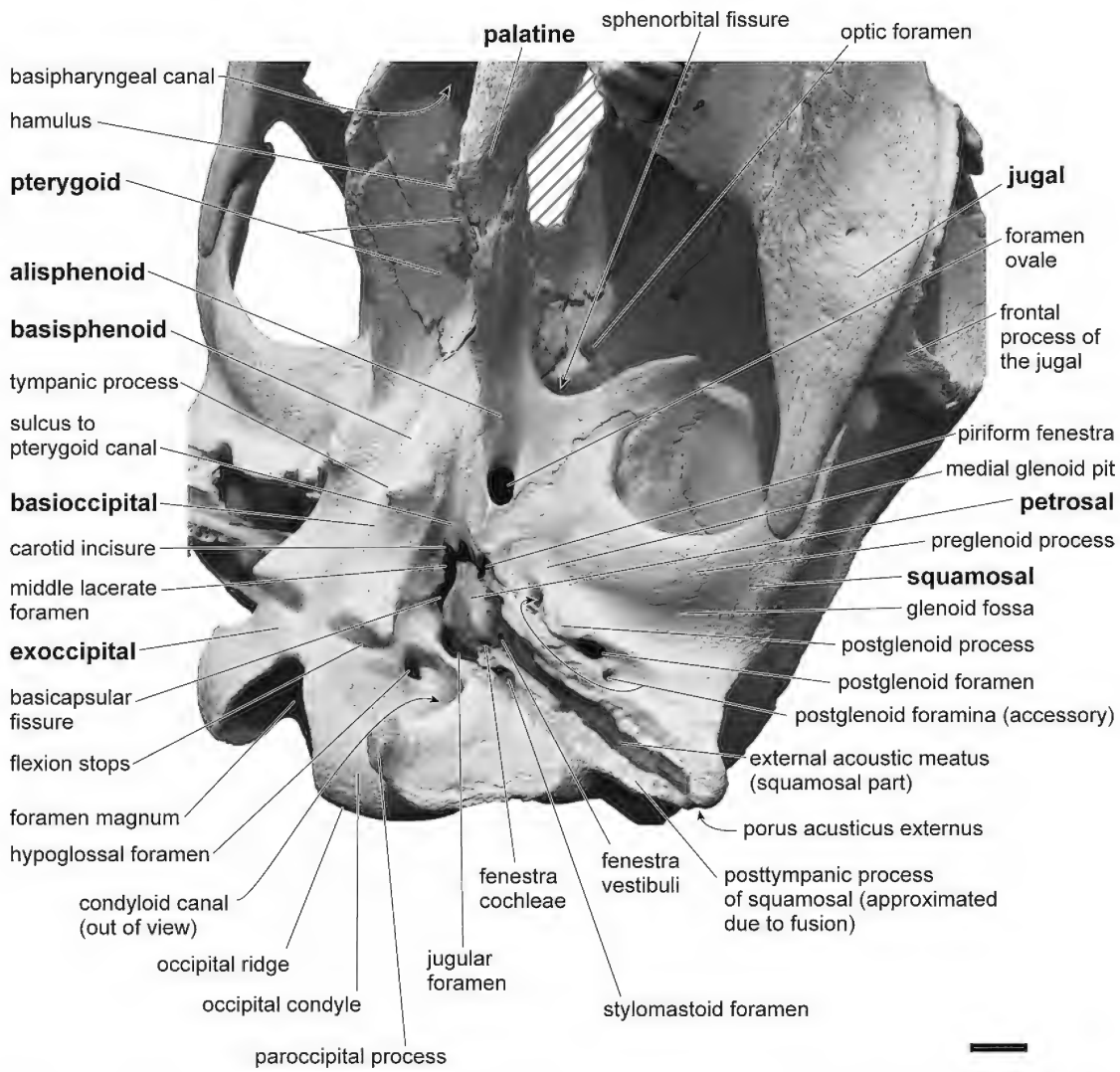

FIGURE 13. Left basicranium of *Bos taurus* (Cetruminantia, Ruminantia, Bovidae; SBU-MAR 14) with bulla removed to reveal petrosal in situ. Scale bar = 1 cm.

crest, the bullar ridge, which follows an anteromedial to posterolateral direction. The bullar ridge starts at the posterior aspect of the styliform process. As the ridge extends toward the posterolateral corner of the bulla, where it terminates posterior to the tympanohyal, it gives rise to several irregular knobs that are not bilaterally symmetrical in shape or number. The bulla forms a deep stylohyal fossa, where it wraps around the inferior end of the tympanohyal but does not completely enclose it posterolaterally. The inferior end of the tympanohyal is slightly flattened and does not project beyond the borders of the stylohyal fossa. A conspicuous semicircular crest on the bulla marks the anterior and anterolateral edges of the stylohyal fossa.

A distinct sulcus marked by sharp edges runs along the alisphenoid between the anterior bulla and the posterior and lateral margins of the basipharyngeal canal terminating at the posterior opening of the pterygoid canal. At the anteromedial edge of the bulla the carotid incisure is vis-

ible with the bulla in place. The anterior carotid foramen is tucked deeply into the anterior aspect of the bulla and is not visible with the bulla in situ. The posterior carotid foramen is also not visible with the bulla in situ and this entry point into the middle ear is marked only by an inconspicuous groove on the bulla itself.

The stylomastoid foramen is a distinct circular opening just lateral to the posterior part of the exposed tympanohyal (fig. 12). The other three borders of the foramen are the exoccipital, the mastoid region of the petrosal, and the external acoustic meatus (less clear in fig. 13, where sutures are obliterated). There is a furrow leading out of the foramen and running along the squamosal posterior to the external acoustic meatus. The external acoustic meatus is longer mediolaterally than is the bulla. A narrow ridge of bone runs the entire length of the external acoustic meatus from the porus acusticus externus to the tympanohyal. This bony ridge projects ventrally from the bulla for several centimeters. The porus acusticus externus is inset medially relative to the lateral edge of the skull. The external acoustic meatus has a number of minute, irregularly positioned small holes (fig. 12). The external acoustic meatus is also fused posteriorly to the mastoid region of the petrosal, to the posttympanic process of the squamosal laterally and posteriorly, and to other parts of the squamosal anteriorly. The sutures are obliterated. At the porus acusticus externus it is apparent that the ectotympanic part of the external acoustic meatus forms a completely circular tube that lies within (and is fused to) a depression on the squamosal. However, due to fusion, this tube cannot easily be removed intact (fig. 11). The bulla is in extensive contact with the petrosal during life and also contacts the basisphenoid/basioccipital area medially. Not shown in the illustrations is the contact between the bulla and the alisphenoid anterolaterally. The internal aspect of the bulla contains numerous chambers of cancellous bone.

With the bulla removed, the large piriform fenestra is exposed between the anterolateral petrosal and the alisphenoid/squamosal (fig. 13). The piriform fenestra is fully contiguous with the carotid foramen, which forms a notch in the midline near the junction between the basisphenoid and basioccipital (suture is obliterated). The carotid incisure is fully confluent with the middle lacerate foramen and the basicapsular fissure. Posterior to this area the petrosal abuts the basioccipital and may be fused. This junction separates the jugular foramen from the basicapsular fissure, and each of those openings leaves small notches in the basisphenoid/basioccipital. The jugular foramen is an elongate oval.

The glenoid fossa is situated on the posterior aspect of the squamosal contribution to the zygomatic arch (fig. 12). The fossa is mediolaterally elongate, with a convex preglenoid process anteriorly and concave area posterolaterally. In the isolated bulla, grooves for the anterior and posterior carotid foramina are inconspicuous. A medial glenoid pit is present. Posterior to the glenoid fossa is a small postglenoid process situated on the medial aspect of the joint. Posterior to the postglenoid process lies the postglenoid foramen adjacent to a medially positioned accessory postglenoid foramen of smaller size. In SBU-MAR 15 these two openings are also joined via a canal posterior to the postglenoid foramen; in SBU-MAR 14, this canal is absent. The larger of the two foramina is situated more medially and directly behind the postglenoid process (this process is shown in situ in fig. 12 and removed to show foramina in fig. 13). Medial to the medial glenoid pit is a scroll of bone (part of the alisphenoid) that lies just anterior to the bulla but does not touch it.

Cetruminantia – Ruminantia – Pecora – Cervidae

Odocoileus virginianus

Figures 11, 14, 15

An illustration of the basicranial aspect of the ear region of *Odocoileus* is found in Edinger and

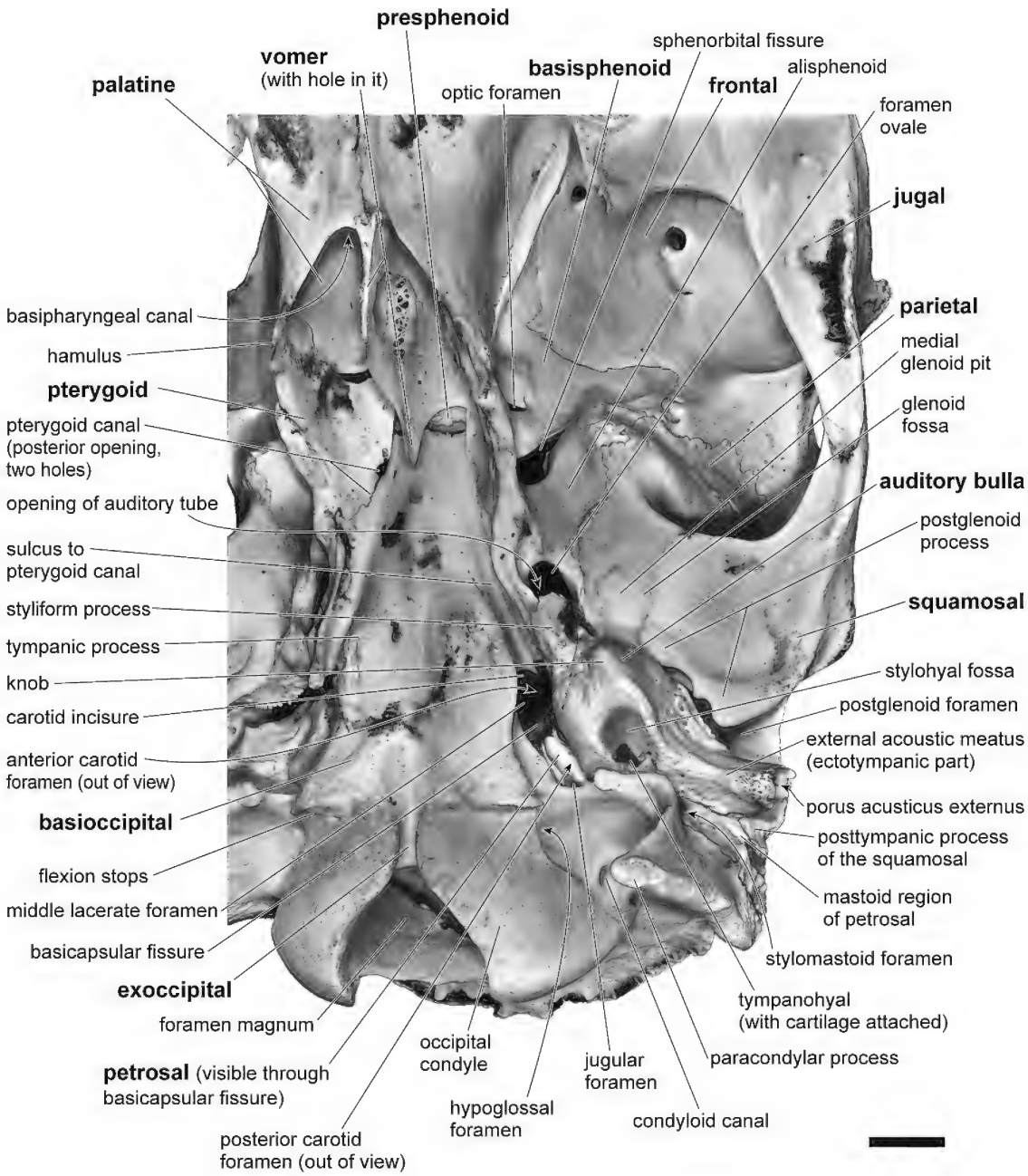

FIGURE 14. Left basicranium of *Odocoileus virginianus* (Cetruminantia, Ruminantia, Cervidae; AMNH-M 244789) with auditory bulla in situ. Scale bar = 1 cm. Photograph: S. Goldberg.

Kitts (1954) with a general discussion of variability in the foramen ovale.

The bulla is relatively loosely attached to the skull in this taxon, essentially held in place by its enclosure of the tympanohyal via the stylohyal fossa (fig. 14). If the tympanohyal is broken, the bulla easily separates from the skull. Figure 15 is an adult skull (SBU-MAR 20) with the bulla and the tympanohyal removed to show the petrosal in situ. The skull preserves sutures very clearly.

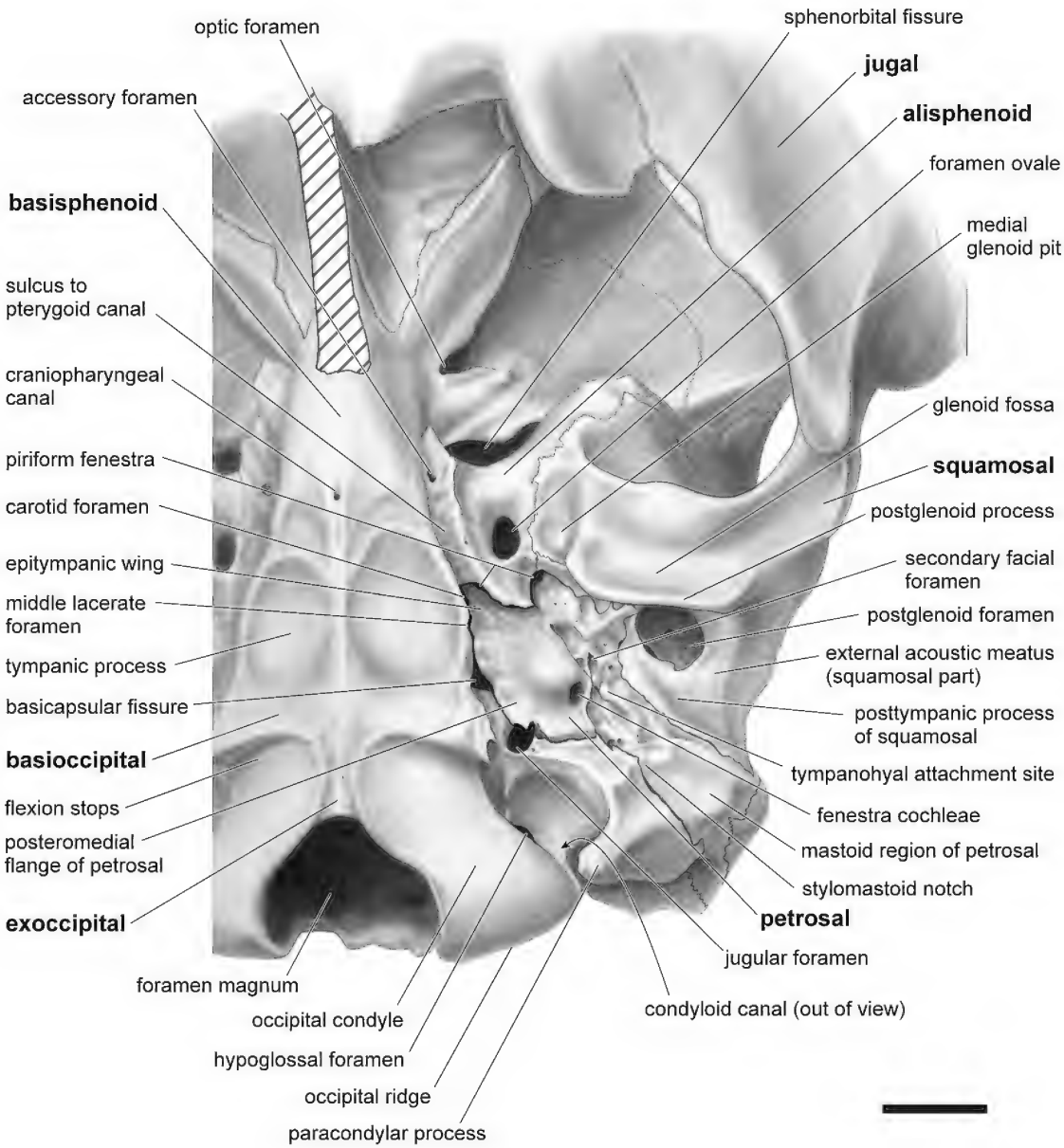

FIGURE 15. Left basicranium of *Odocoileus virginianus* (Cetruminantia, Ruminantia, Cervidae; SBU-MAR 20) with auditory bulla removed to reveal petrosal in situ. Scale bar = 1 cm. Artist: U. Kikutani.

AMNH-M 244789 is an adult specimen and demonstrates the skull with the bulla in situ.

Both figures 14 and 15 show several features of the orbit; the optic canal is generally round but reaches a point at its inferior aspect. The optic foramen lies anterior and slightly superior to the sphenorbital fissure. The large sphenorbital fissure is teardrop shaped with the apex positioned superolaterally at the junction of the parietal, alisphenoid, and basisphenoid. At the base of the sphenorbital fissure is the very small anterior opening of the pterygoid canal. Directly posterior to the sphenorbital fissure is the foramen ovale, which is contained entirely within the alisphenoid,

however, the lateral margin of the foramen ovale very closely approximates the alisphenoid-squamosal suture. The suture between the alisphenoid and the basisphenoid is obliterated.

The posterior aspect of the hard palate is flat (fig. 14). The posterior spine is absent on the palate and the medial edges of the palatine bones do not extend as far posteriorly as do the lateral edges. The vomer is exposed in the basipharygneal canal, extending well past the posterior edge of the palatine bones and almost as far posteriorly as the posterior edge of the entopterygoid process. The posterior aspect of the vomer terminates as a small, pointed projection of bone and this extends posterior to the presphenoid-basisphenoid suture (fig. 14). This projection is only partially in contact with the roof of the basipharyngeal canal. The presphenoid has a small exposure in the superior aspect of the basipharyngeal canal. The margins of the pterygoid versus the palatine and alisphenoid bones are very clear. The entopterygoid process forms a small hamulus with a blunt end, and the hamulus is essentially level with the palate (fig. 14). There is almost no development of a pterygoid fossa and little development of an ectopterygoid process. The pterygoid canal appears to have two posterior openings (one anterior to the other) that unite to open together at the anterior opening of the pterygoid canal in the orbit (fig. 14). The more anterior of these passes directly into the orbit, and the more posterior travels along the superior part of the pterygoid toward the orbit. There is no craniopharyngeal canal.

In the midline, there is a small basipharyngeal canal (fig. 15). The tympanic processes are circular, roughened areas that do not project significantly from the skull base (fig. 14). These processes have no contact with the auditory bulla. Flexion stops at the anterior aspect of the occipital condyles are very pronounced and deeply excavated (fig. 15). The flexion stops abut the tympanic processes posteriorly. The occipital condyles approximate each other at the anterior midline but do not touch. They have distinct ventral and posterior surfaces that meet at a right angle forming an occipital ridge. The paracondylar process is a triangular plate in lateral view and is widest superiorly at its base where it contacts the auditory bulla. The apex of the process extends as far ventrally as the alveolar line of the upper dentition. The process hooks slightly medially from superior to inferior (particularly clear when seen in posterior view). The paracondylar process terminates in a small knob (fig. 14). These processes lie adjacent to the mastoid region of the petrosal, which is exposed with clear sutures between it and the exoccipital and squamosal.

There is both a hypoglossal foramen and a condyloid canal (fig. 15). Both are positioned superior to the occipital condyles and are partially hidden by them. The hypoglossal foramen is positioned relatively anterior and medial; it is a direct opening to the superior aspect of the foramen magnum. The condyloid canal is adjacent to the hypoglossal canal and runs more extensively within the exoccipital before opening endocranially. The condyloid canals are variable and tend to be larger externally than internally and open in a nonbilaterally symmetrical fashion on the deep surface of the condyle.

Several foramina and channels are visible with the bulla in situ (fig. 14). Starting anteriorly, medial to the foramen ovale (described above), there is a distinct sulcus running near the junction of the basisphenoid and the alisphenoid. A sharp crest on the alisphenoid marks the sulcus laterally, and the sulcus runs from the middle ear toward the ptergygoid fossa, eventually leading to the posterior opening of the pterygoid canal. The sulcus is most pronounced between the middle ear and the pterygoid fossa, becoming much more faint as it approaches the posterior opening of the pterygoid canal.

The bulla is flask shaped with a spherical medial portion (figs. 11, 14). A tube-shaped external acoustic meatus projects posteriorly and terminates at the lateral edge of the skull;

there is a spike-shaped styliform process. The styliform process extends only as far ventrally as the bulla or a little beyond. The styliform process is flattened anteriorly and concave on its anteromedial surface. The bulla has a number of irregularly positioned pin-sized holes. The only other distinctive feature of the bulla is a knob projecting from its center at the most ventral part of the bulla. A ridge extends posterolaterally from this knob and marks the lateral edge of the stylohyal fossa (fig. 14). The bulla surrounds the tympanohyal only partially, such that the tympanohyal is partly exposed posterolaterally. The tympanohyal has a flattened inferior tip and does not project ventral to the bulla. The stylomastoid notch lies directly posterolateral to the tympanohyal and there is no pronounced sulcus for the facial nerve on the external aspect of the stylomastoid foramen.

The anterior carotid foramen is not visible with the bulla in situ because the foramen is positioned very deeply between the petrosal and bulla. The posterior carotid foramen is distinguished only by a slight indentation in the bulla near the jugular foramen and is also essentially out of view with the bulla in situ (figs 11, 14). However, when the bulla is in situ, the carotid foramen, middle lacerate foramen, basicapsular fissure, and jugular foramen are all visible and contiguous (fig. 14). The petrosal and bulla as a unit are not appressed closely to midline skull structures. The petrosal is also partially exposed even with the bulla in place, and specifically, its pars cochlearis lacks extensive contact with the surrounding alisphenoid, basisphenoid, basioccipital, and exoccipital. It is the pars canalicularis of the petrosal, particularly the mastoid region, that is wedged firmly between the exoccipital and squamosal (sutures remain visible). The contact between the pars canalicularis of the petrosal and the squamosal also contributes to holding the petrosal in place.

With the bulla removed it is apparent that the piriform fenestra is bordered by the alisphenoid and squamosal anteriorly and by the petrosal posteriorly (fig. 15). This fenestra is elongate, extending from the basisphenoid medially to the squamosal laterally, and is divided in two by a posteriorly directed triangular process from the alisphenoid. The carotid foramen lies at the anteromedial corner of the petrosal between the lateral margin of the basisphenoid/basioccipital and the jagged anterior edges of the flanges of the pars cochlearis of the petrosal. There is a very narrow middle lacerate foramen posterior to the carotid foramen and contiguous with it. The basicapsular fissure is an elongate, broad oval. A projection from the lateral margin of the basioccipital/exoccipital (the suture is obliterated) meets the posteromedial flange of the petrosal (the two structures just barely touch) and separates the basicapsular fissure from the jugular foramen in some specimens (SBU-MAR 20), but the entire area is much more open in others (AMNH-M 244789). The jugular foramen is round with an additional small, slitlike continuation at its lateral edge that extends posterior to the fenestra cochleae of the petrosal (fig. 15).

When the bulla is removed it is apparent that the external acoustic meatus forms a complete tube from the ectotympanic alone (fig. 11). The bone of the tube is roughened in places, but the tube does not fuse to the squamosal against which it lies. The part of the bulla adjacent to the ectotympanic annulus is marked by numerous small foramina. The bulla itself is completely hollow and devoid of bony struts or cancellous structures. The canal for the auditory tube is relatively broad with roughened edges and terminates in the styliform process (which varies in size between the two specimens examined; fig. 11 shows a relatively small styloid process). Canals that mark the places where the anterior and posterior carotid foramina would be formed as the bulla met the petrosal are very subtle. The position of the posterior carotid foramen in SBU-MAR 20 is marked by an irregular small hook of bone.

The glenoid fossa is convex anteriorly (the preglenoid process) and concave posteriorly (fig.

15). The postglenoid process is positioned predominantly toward the medial aspect of the joint in SBU-MAR 20 and runs posterolateral to anteromedial. There is a medial glenoid pit at the medial aspect of the glenoid fossa. When the skull is articulated with the mandible no part of the mandibular condyle contacts this pit. The postglenoid foramen is large and partly obscured by the bulla and the postglenoid process.

Cetruminantia – Ruminantia – Tragulidae

Tragulus javanicus and *T. napu*

Figures 16–18

The basicranium of *Tragulus javanicus* has been figured (Starck, 1995: 1020), but none of the structures are labeled; Kampen (1905) provided details on the auditory bulla of Tragulidae. Two specimens are figured here, one of *T. napu* with the bulla in situ (fig. 16) and one of *T. javanicus* with the bulla removed (fig. 17). The bulla is typically very tightly held in place or even fused to surrounding bones by maturity (e.g., AMNH-M 188310), and the view of the petrosal in situ without the bulla has been possible because the bulla was detached in the subadult *T. javanicus* specimen (AMNH-M 102091), which has unerupted upper and lower third molars. Observations on the adult anatomy with the bulla in situ were supplemented by examination of AMNH-M 32652.

Several posterior orbit structures are visible in figures 16 and 17. The optic foramen is oval and positioned anterosuperiorly relative to the sphenorbital fissure. The sphenorbital fissure is teardrop shaped, coming to a point at its superior aspect and it appears to be contained entirely within the alisphenoid.

A variably present accessory foramen lies anteromedially adjacent to the foramen ovale (only in the specimen in fig. 17) near the junction of the alisphenoid and the basisphenoid. The accessory foramen is present bilaterally in some specimens and absent in others. On the left side this foramen appears to open at the posterior base of the sphenorbital fissure and to have connections into the body of the sphenoid itself, however, on the right side the accessory foramen enters the body of the sphenoid but does not appear to emerge. This accessory foramen is absent in the mature AMNH-M 188310. A distinct pterygoid canal is either absent or very small, although specimens AMNH-M 188310 and 32652 have small holes inferior to the sphenorbital fissure (not illustrated), but it is not apparent that these foramina connect to openings more posteriorly.

Both figures 16 and 17 show the posterior aspect of the basipharyngeal canal. The vomer is not visible because it terminates anterior to the posterior end of the palatine bone and anterior to the presphenoid-basisphenoid suture. The pterygoid bones are not preserved in the subadult but are preserved in the mature specimen. The ento- and ectopterygoid processes are approximately the same size, both projecting only a small distance posterolaterally at their ventral margins. There are distinct sutures indicating where the palatine bone ends posteriorly and how the pterygoid and the alisphenoid contribute to the posterior tips of the pterygoid processes. There is little development of a pterygoid fossa; there is only a small space at the inferior aspect of the two pterygoid processes. The hamulus has a convex ventral border and projects posterolaterally, terminating in a subtle hook. The hamulus does not project ventrally to a significant distance relative to the palate. The posterior edge of the hard palate is straight where the two palatine bones meet in the midline, and the posterior parts of the palatine bones lack a nasal spine.

The midline has a craniopharyngeal canal in AMNH-M 10291 and 188310 (fig. 17; out of view in fig. 16) just anterior to the tympanic processes. The tympanic processes are elongate, oval bumps situated primarily on the basioccipital but also extending onto the basisphenoid. The two processes are more closely approximated to each other posteriorly than anteriorly. The tympanic processes are situated relatively close to the mid-

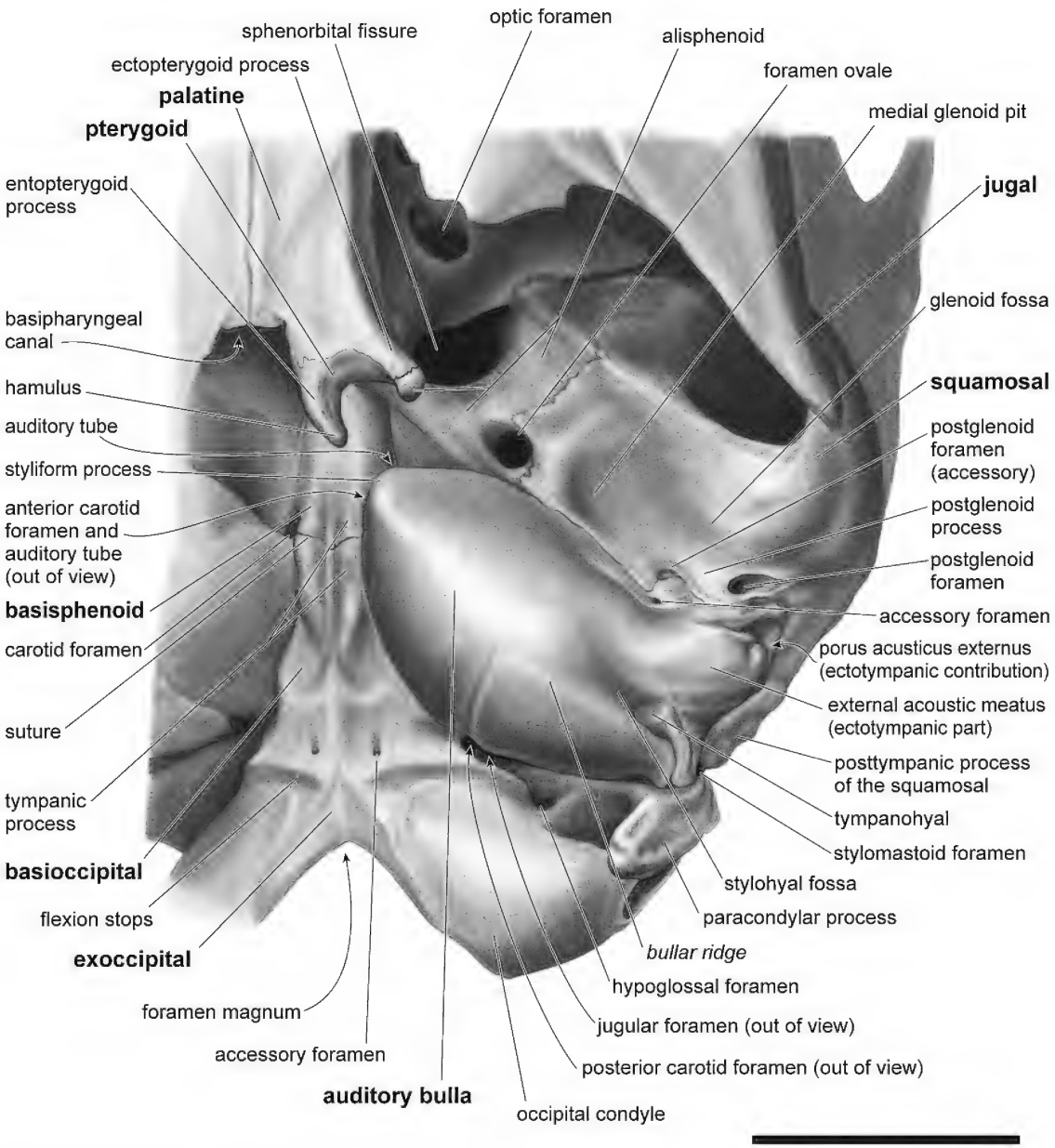

FIGURE 16. Left basicranium of *Tragulus napu* (Cetruminantia, Ruminantia, Tragulidae; AMNH-M 188310) with bulla in situ. Scale bar = 1 cm. Artist: U. Kikutani.

line (yet each remains distinct from the other) and they do not contact the auditory bulla.

The occipital condyles of the exoccipital are distinctly separate anteriorly. They have gentle flexion stops at their anterior extreme. The occipital condyle has both a ventral and a posterior aspect, and a very subtle occipital ridge marks the transition between the two surfaces. The paracondylar process is a simple projection that extends straight down from the skull base. It does not extend as far ventrally as the ventral edge of the auditory bulla. An accessory foramen (fig. 17) at the base of the paracondylar process is also present in the immature speci-

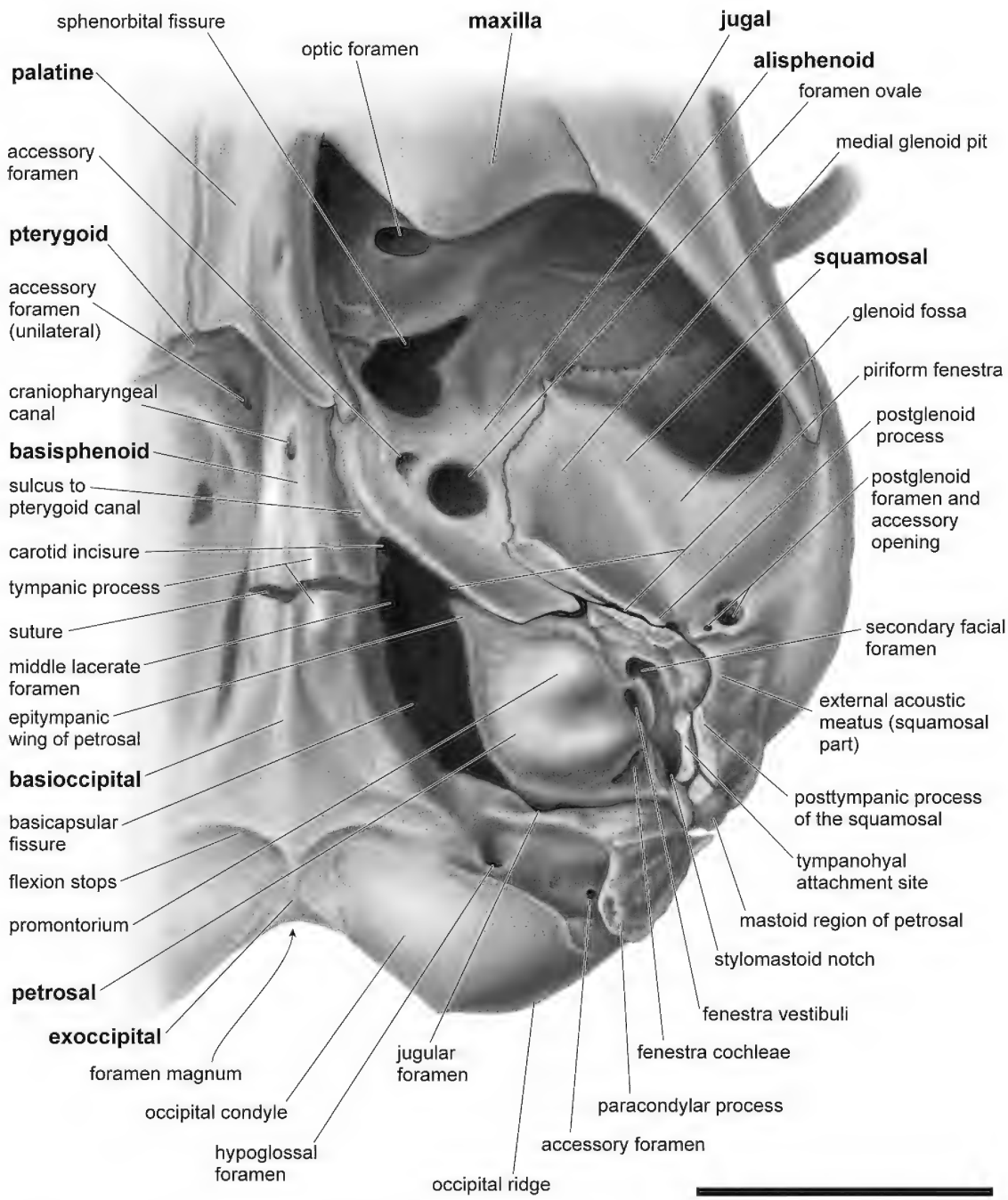

FIGURE 17. Left basicranium of *Tragulus javanicus* (Cetruminantia, Ruminantia, Tragulidae; AMNH-M 102091) with bulla removed to reveal petrosal in situ. Scale bar = 1 cm. Artist: U. Kikutani.

men but absent in the mature specimen. The hypoglossal foramen is posteromedial to the jugular foramen. It is a single hole somewhat deeply set and separated from the jugular foramen by a distinct ridge. Visible in the foramen magnum there are some extremely small foramina (three on the left and one on the right; out of view in the illustrations) on the internal surface of the occipital condyle (AMNH-M 188310). These appear to terminate within the bone. A condylar foramen that actually pierces the condyle is absent in both specimens.

The auditory bulla is ovoid, coming to a small pointed styliform process at its anteromedial edge (figs. 16, 18). The surface of the bone is smooth and the bulla lacks a conspicuous exit for the auditory tube. The most ventral aspect of the bulla forms a bullar ridge along its length that sweeps from the anteromedial to the posterolateral extremes of the bone terminating posterior to the tympanohyal. The tympanohyal invaginates the posterolateral edge of the bulla where it is tightly held in a stylohyal fossa that occupies the posterolateral one-third of the bulla (fig. 16). There is some fusion of the tympanohyal and the bulla superiorly. The bulla does not completely surround the tympanohyal, even in mature individuals. The tympanohyal is also appressed to the paracondylar process of the exoccipital. The tip of the tympanohyal is flat and broad and distinctly exposed emerging from the stylohyal fossa. The external acoustic meatus is a distinct tube that does not quite extend to the lateral edge of the skull but terminates directly posterior to the postglenoid foramen. The ectotympanic forms a complete tube of bone that sits within a shallow depression on the squamosal. The bulla contains a small accessory foramen on its anterolateral aspect (fig. 16). The stylomastoid foramen is a small, circular hole formed by the bulla abutting the mastoid region of the petrosal. It is located posterolateral to the tympanohyal and anterolateral to the paracondylar process. The paracondylar process broadens at the superior end and contacts the auditory bulla.

Medially and posteromedially, the bulla is tightly appressed to the basioccipital and exoccipital such that the wide openings between the petrosal and these other bones, described below, are almost completely obscured. In many specimens (e.g., AMNH-M 188310) the bulla is so tightly appressed to surrounding bones that there is only one conspicuous opening between the bulla and the basioccipital in ventral view of the skull: a confluent opening for the posterior carotid foramen and the jugular foramen (fig. 16). The shape of this foramen is somewhat variable. It is a small opening externally in AMNH-M 188310 that attenuates as a slit posterolaterally, but by contrast, in AMNH-M 32652 (not illustrated) there is a large, confluent pair of openings where the posterior carotid foramen and the jugular foramen would typically lie. Entry to this foramen at the posteromedial aspect of the bulla is distinguished by a gentle furrow on the bulla itself, a furrow that starts ventrally, medial to the bullar ridge, and disappears into the foramen (fig. 18). Besides the midline bones mentioned above, the bulla also makes contact with the alisphenoid and the petrosal, and its external acoustic meatus has extensive contact with the squamosal. The anterior carotid foramen is tucked deep within the anterosuperior aspect of the bulla and not visible with the petrosal in situ (see fig. 16). It is formed between the bulla and the petrosal. The groove for the auditory tube is not very distinct from the anterior opening of the carotid foramen (figs. 16, 18).

With the bulla removed the relationship of the petrosal to the surrounding bones can be seen (fig. 17). As noted above, the foramen ovale is contained entirely within the alisphenoid; it is not part of the petrosal complex. A large space separates the petrosal from the alisphenoid, basisphenoid, and basioccipital such that several openings into the skull are contiguous. The piriform fenestra is a gracile slit just lateral to the pointed epitympanic wing of the petrosal. It lies between the petrosal and the alisphenoid and squamosal. Posteromedial to the foramen ovale and on the medial side of the epitympanic wing

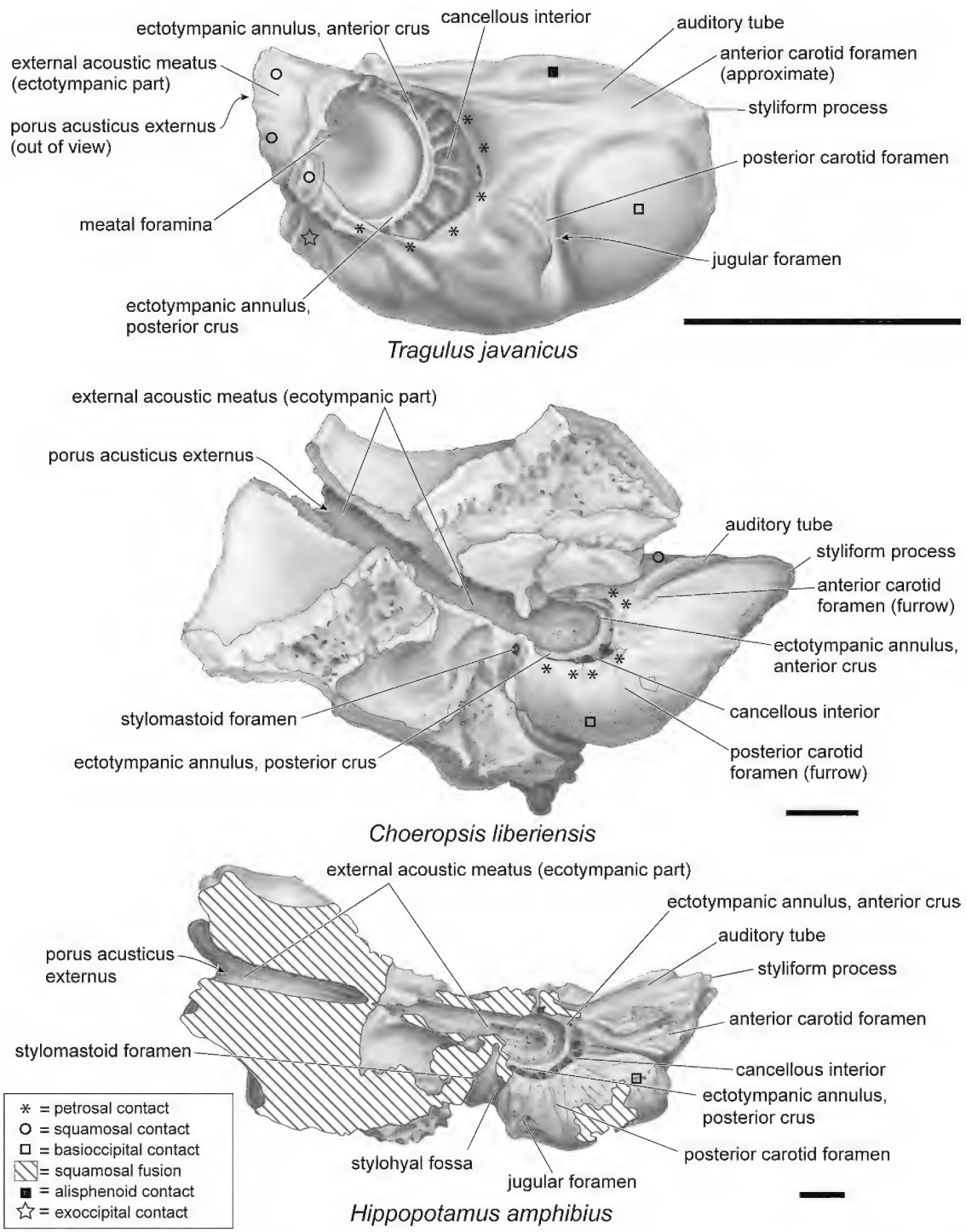

FIGURE 18. Left auditory bullae of *Tragulus javanicus* (Ruminantiamorpha, Ruminantia, AMNH-M 102091), *Choeropsis liberiensis* (Cetancodonta, Hippopotamidae, UCR 3116) and *Hippopotamus amphibius* (Cetancodonta, Hippopotamidae, AMNH 24289). Scale bar = 1 cm. Artists: U. Kikutani (*Tragulus*), C. Lodge (*Choeropsis* and *Hippopotamus*).

is the carotid incisure at the anteriormost aspect of the large space between the petrosal and midline structures. More posteriorly there are no distinct boundaries for the middle lacerate foramen or the basicapsular fissure, but the space is widely opened. The basicapsular fissure is distinct from the jugular foramen with the exoccipital intervening between the two openings but not quite touching the petrosal and not completely closing off the jugular foramen from more anterior openings. The jugular foramen is elongate mediolaterally. The mastoid region of the petrosal is exposed between the exoccipital (just anterior to the paracondylar process) and the squamosal.

In isolation the smooth-surfaced bulla reveals the scroll of bone comprising the external acoustic meatus (fig. 18). The length of the meatus is relatively short compared to the full mediolateral length of the bulla. The inside of the bulla is filled with cancellous bone forming numerous chambers. The region adjacent to the ectotympanic ring has extensive contact with the petrosal. As noted above, the bullar contributions to the anterior carotid foramen and the auditory tube are not marked by strong grooves; its contribution to the posterior carotid foramina is more pronounced.

The glenoid fossa is situated entirely on the squamosal; it is mediolaterally elongate, convex laterally, and concave medially forming a medial glenoid pit (figs. 16, 17). Posterior to the medial glenoid pit a scroll of squamosal curves ventrally and wraps against the bulla. The lateral aspect of the glenoid fossa is situated on the zygomatic arch and not on the braincase. There is a single, small, circular postglenoid foramen, visible whether the bulla is in situ or not. On the left side of the immature specimen there is also a small accessory foramen adjacent to this.

Cetancodonta – Hippopotamidae

Choeropsis liberiensis

Figures 18–20

Aspects of the ear region of *Choeropsis liberiensis* have been described by several authors (Leidy, 1853; Pearson, 1927; 1929; Orliac et al., 2014) with Orliac et al. (2014) providing CT-based reconstructions of cranial vasculature in this region.

The bulla of *Choeropsis liberiensis* is very tightly fused to the skull particularly in the region of the external acoustic meatus (fig. 19). No specimen was available with the bulla removed and the petrosal in situ (a specimen with the petrosal completely removed is described in O'Leary, 2010). Nonetheless, a number of basicranial features can be seen in the adult specimen AMNH-M 81899, which is described below, supplemented by information from AMNH-M 148452 and from the dissected bulla of specimen UCR 3116.

The posterior orbit and palate are visible in figure 19. The sphenorbital fissure is relatively round and is set posterior and slightly lateral to the much smaller optic foramen. There are several very small openings anterior to the sphenorbital fissure, one of which may be the anterior opening of the pterygoid canal, but it is too small to verify continuity with the posterior opening of the pterygoid canal using a typical probe (more on that below). The postorbital process of the frontal juts toward the orbit but does not meet the jugal.

The posterior aspect of the palate has paired posterior spines of irregular shape and size, each terminating in a small knob (fig. 19). The plane of the palate is very flat with a roughening in the midline at the suture between the two palatine bones. AMNH-M 81899 has some asymmetry of the major palatine foramina; there is one on each side at the anterior aspect of the suture between the palatine and the maxilla and a third, on the right side only, that is more posterior and exclusively within the palatine (this last one is visible in fig. 19, which is the right side [drawing reversed]).

Visible in the roof of the basipharyngeal canal is the posterior end of the vomer, as are faint indications of a suture between the vomer and the pterygoids (fig. 19). The presphenoid is either not exposed or its suture with the basisphenoid is obliterated. The sutures between the pterygoids and the alisphenoids in the lateral walls of the basipharyngeal canals are almost entirely

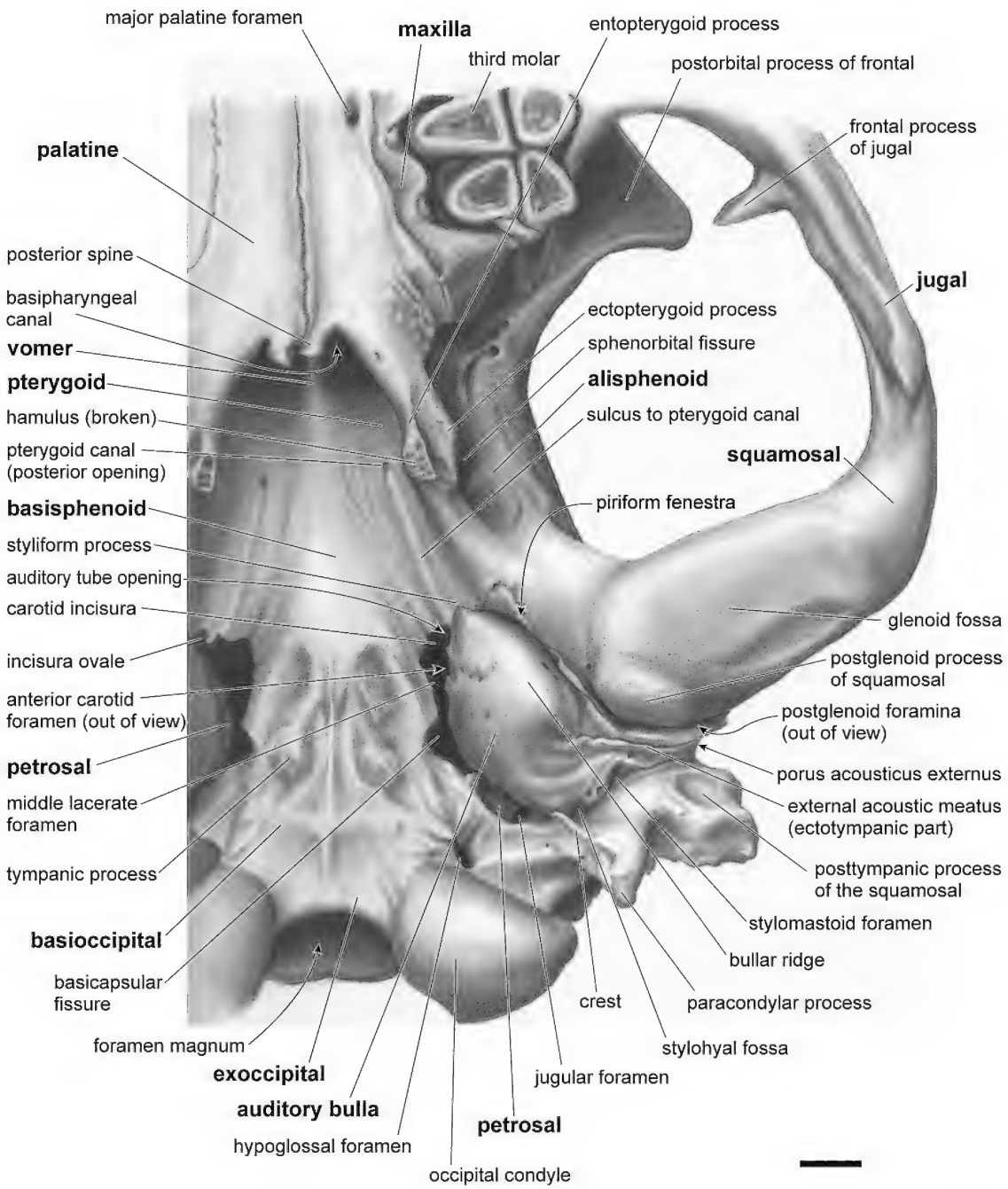

FIGURE 19. Left basicranium of *Choeropsis liberiensis* (Cetancodonta, Hippopotamidae, AMNH-M 81899) with auditory bulla in situ. Right side of specimen reversed. Scale bar = 1 cm. Artist: U. Kikutani.

obliterated, although at the posterior edge of the pterygoid, the separation between pterygoid and the alisphenoid is clear. In the roof of the basipharyngeal canal almost halfway between the midline and the lateral walls are distinct posterior openings for the pterygoid canals. Although unambiguous, these openings are so small that their continuity with an anterior opening cannot be easily verified with a probe. Running posteriorly from them to the middle ear region is a distinct and elongate sulcus (fig. 19). There is little development of a pterygoid fossa, with the ento- and ectopterygoid processes being clearly distinct only at their ventral ends. The entopterygoid process terminates in a roughened ridge that runs anteroposteriorly. The hamulus (partially broken in fig. 19; observations based on AMNH-M 148452) extends ventrally well below the entopterygoid process. It is oriented in a parasagittal plane and forms a hook posteriorly and terminates in a knob.

In the midline a craniopharyngeal canal is absent and the suture between the basisphenoid and the basioccipital is obliterated (fig. 19). The basioccipital and basisphenoid bones have an overall sculpted appearance. The tympanic processes are distinct round knobs that lie just posterior to bilateral oval depressions with distinct outlines at their anterior edges. The occipital condyles are widely separated and lack both flexion stops and a distinct occipital ridge, although the condyles do have both a ventral and a posterior surface. There is one large hypoglossal foramen just anterolateral to the anterior aspect of the occipital condyle. It opens into the foramen magnum; the condyloid canal is absent. The paracondylar process is a small, straight structure that is of relatively uniform size from its base to its ventral tip. It extends ventral to the bulla and, in lateral view, angles posteriorly. At its base superiorly, the paracondylar process contacts the bulla via a small, sharp crest.

As noted above, the auditory bulla is held in place extremely tightly, primarily by full fusion of the elongate external acoustic meatus to the postglenoid and posttympanic processes of the squamosal (fig. 19). The bulla is ovoid and oriented with its long axis anteromedial to posterolateral. Medially the bulla contacts the overlying petrosal extensively but not the alisphenoid, basisphenoid, or basioccipital (fig. 18). The bulla itself has a number of pinhole-sized openings (the largest of which is at the anterolateral aspect of the bulla and is out of view in the illustrations). It also has some areas of jagged-textured bone posteriorly. The external acoustic meatus is as wide as the bulla mediolaterally; the meatus wraps onto the lateral side of the skull such that the porus acusticus externus is substantially more superior than is the middle ear. The external acoustic meatus has mediolaterally elongate crests of bone on its ventral surface. The posttympanic process of the squamosal is not only fused to

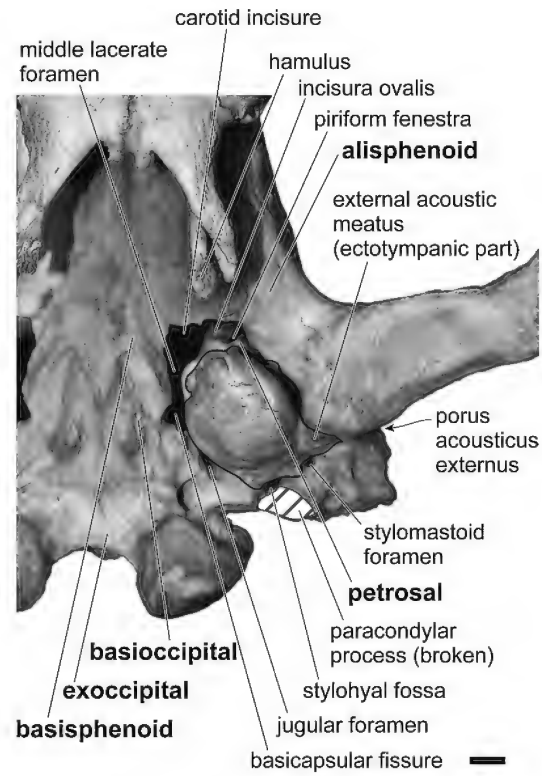

FIGURE 20. Left basicranium of *Choeropsis liberiensis* (Cetancodonta, Hippopotamidae, AMNH-M 81899), angled close-up to show space between petrosal and surrounding bones. Scale bar = 1 cm.

the external acoustic meatus, but also to the exoccipital. The styliform process of the bulla is a small pointed process (figs. 18, 19). Following it superiorly onto the medial side of the bulla, a channel emerges on the dorsomedial aspect of the bulla that marks the opening for the auditory tube (fig. 18). This channel is marked by a strong crest. Running posteriorly from the styliform process on the external (ventral) surface of the bulla is a gentle bullar ridge that follows the long axis of the bulla. The ridge terminates in one of the crests, noted above, that runs along the ventral surface of the external acoustic meatus. The crest lies anterior to the stylomastoid foramen. Sutures indicate that the anterior two-thirds of the edge of the stylomastoid foramen are formed by the bulla and its posterior one-third by the exoccipital. There is no sulcus external to the stylomastoid foramen. The stylohyal fossa is posteromedial to the stylomastoid foramen, and is a gentle depression in the posterior bulla. The stylohyal fossa is bordered posteriorly by the exoccipital, and the crest of bone from the paracondylar process (noted above) marks the medial border of the fossa. On the right side of the specimen (the left is slightly broken in this area) there is a small prong of bone deep within the stylohyal fossa (not visible in illustrations). This structure appears to be a very small, recessed tympanohyal and it rests against the exoccipital. There are no particular grooves or channels marking the posterior carotid foramen whether the bulla is in situ or removed. The anterior carotid foramen appears to be marked only by a slight indentation in the bulla and a small crest adjacent to it.

Anteromedially, medially, and posteromedially there is a wide and contiguous space between the petrosal-bulla complex and the surrounding bones (fig. 19). The piriform fenestra is a wide area that blends with the incisura ovalis such that there is little distinction between them (fig. 20). Similarly the carotid incisure/foramen is distinguished only by a small, medially oriented notch in the basisphenoid. This notch is fully open to the middle lacerate foramen and the basicapsular fissure. There is a slight approximation of the basioccipital/exoccipital and the petrosal/bulla complex between the basicapsular fissure and the jugular foramen, but these openings are still confluent. The jugular foramen is a large anteromedially to posterolaterally oriented opening that is fully visible with the bulla in place (figs. 19, 20).

When the bulla is viewed in isolation (fig. 18) it is clear that the ecotympanic annulus is one continuous structure with indistinct divisions between the two crura. The internal aspect of the bulla is cancellous and the bulla has extensive contact with the petrosal. The auditory tube is marked by a distinct trough, but the anterior and posterior carotid foramina leave only indistinct marks on the bulla.

The glenoid fossa has an elongate, oval outline and is gently concave along its orientation from anterolateral to posteromedial (fig. 19). There is no preglenoid process. The postglenoid process is a knob that lies at the posteromedial extreme of the joint only. There is no medial glenoid pit. A distinct postglenoid foramen is absent, as has been noted in much greater detail using micro CT scan–based reconstructions by Orliac et al. (2014). Those authors observed that while an opening remains patent, often through multiple minute passageways, there is no "fully individualized" postglenoid foramen in *Choeropsis* (Orliac et al., 2014: 2). Such detail cannot be seen in the illustrations here, but in the specimens themselves there are small slits between the external acoustic meatus and the postglenoid process that most likely led to the passageways to the endocranium identified by Orliac et al. (2014). These slits are too small to penetrate with standard probes.

Hippopotamus amphibius

Figures 18, 21, 22

The ear region of *Hippopotamus* and its closely related fossil relatives has been described by several authors (Leidy, 1853; Kampen, 1905; Pear-

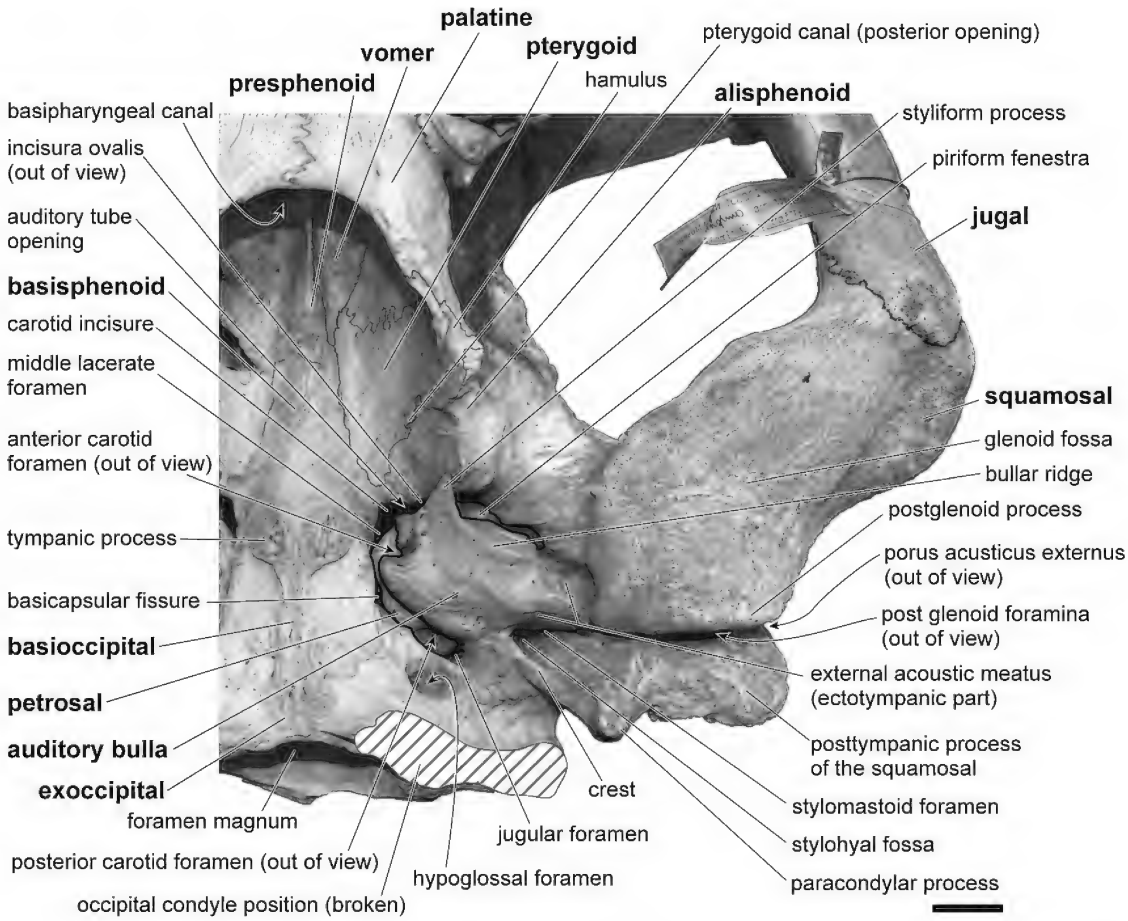

FIGURE 21. Left basicranium of *Hippopotamus amphibius* (Cetancodonta, Hippopotamidae, USNM-M 182395) with bulla in situ, petrosal is visible through the jugular foramen. Digitally reversed from right side. Scale bar = 1 cm.

son, 1927; 1929; Orliac et al., 2014; Rakotovao et al., 2014) with Orliac et al. (2014) providing CT-based reconstructions of cranial vasculature.

USNM-M 182395, an adult specimen, has the bulla in situ on the right side and removed on the left side (fig. 21). I describe both sides below. Both occipital condyles have previously been removed prior to this study as have parts of the left pterygoid bone and left squamosal. Additional information, such as details on the occipital condyles, was observed on USNM-M 162981 and AMNH M-24289.

The bulla in this taxon is held firmly in place laterally and posteriorly with the external acoustic meatus fused to the squamosal laterally and the bulla fused to the exoccipital posteriorly (fig. 21). Exposure of the petrosal required sawing the bulla off at the medial edge of the external acoustic meatus.

The sphenorbital fissure can be seen in figure 22; it is an oval opening with the long axis oriented superomedially to inferolaterally. It is substantially larger than the optic foramen (not shown) and lies inferolateral to it. The anterior opening of the pterygoid canal appears to be approximately 10 cm anterior to the sphenorbital fissure, at the superior aspect of the exposure of the pterygoid bone within the orbit. It is not apparent where the posterior opening of this canal lies (if it is present at all) even though the

pterygoids are well exposed on the sides and roof of the basipharyngeal canal. The thin pterygoid bones extend posteriorly from the basipharyngeal canal almost to the carotid foramen/incisure. The entopterygoid process that gives rise to the hamulus is not well developed, nor is there a clearly differentiated ectoptyergoid process projecting from the alisphenoid (fig. 21). Thus, there is almost no pterygoid fossa except for a small invagination immediately lateral to the hamulus. The hamulus does not extend far superiorly. The vomer emerges posteriorly from the basipharyngeal canal, and its right and left alae each terminate as a point and diverge in the midline exposing the overlying presphenoid (fig. 21). The pterygoids each taper to a point posteriorly adjacent to the location of the very small posterior opening of the pterygoid canal (fig. 21). There is no particularly distinct sulcus running between this opening and the middle ear. The following sutures are not typically visible in the basicranial view of adult specimens: basisphenoid-basioccipital, alisphenoid-squamosal, and basioccipital-exoccipital. The craniopharyngeal canal is absent (fig. 22). Two round, knob-shaped tympanic processes lie immediately adjacent to the bulla and most likely spanned the basisphenoid-basioccipital junction. These processes have a rough texture with numerous small bumps. The tympanic processes lie medial to the lateral edge of the basisphenoid-basioccipital, and they do not contact the bulla. The knobs are in contact with each other posteriorly and give rise to a median crest that extends posteriorly from the point at which they meet. There is a single hypoglossal foramen on each side that is almost as large as the jugular foramen and gives very direct passage into the foramen magnum (figs. 21, 22). The occipital condyles (not figured) are smoothly convex and exposed on the ventral and posterior surfaces of the skull. There is no distinct occipital ridge. The anterior borders of the occipital condyles are well separated on the ventral surface of the skull and flexion stops are absent. There is no regularly positioned, distinct condylar foramen, although parts of the occiput are pocked with small, irregularly sized and spaced foramina. The paracondylar process is small and triangular shaped. It projects downward with a slight posterior inclination and comes to a knob-shaped point inferiorly. The medial border of the paracondylar process is connected to the bulla by a bony ridge, and the bulla and the exoccipital fuse at the base of the paracondylar process.

The external surface of the bulla has a roughened texture; it is marked with a few spikes of bone and pocked with tiny foramina (fig. 21). The bulla is ovoid with the long axis running from anteromedial to posterolateral. At the anteromedial edge there is a flattened, triangular styliform process. From the ventral tip of the styliform process extends a sharp bullar ridge that runs to the posterolateral corner of the bulla, where the external acoustic meatus disappears between the postglenoid and posttympanic processes of the squamosal bone. The bullar ridge is briefly truncated about one-third of the distance from the posteromedial corner of the bulla. Posterior to the bullar ridge is a deep, columnar-shaped, angled passageway that contains both the stylohyal fossa medially and the stylomastoid foramen laterally. This passageway is set so deeply that it is somewhat obscured in figure 21. The ventral end of the tympanohyal is visible only by looking directly into this opening. The tympanohyal has as a small, circular, and flattened tip. The stylohyal fossa is a very shallow excavation in the bulla; the bulla barely conforms to the tympanohyal at all, contacting it only on its anterior surface where the two structures may even be fused. It appears that a full bony separation between the stylohyal fossa and the stylomastoid foramen is absent. The paracondylar processes are short structures with a wide base superiorly that extend only a short distance inferior to the bulla in lateral view. Crests run between these processes and fuse to the bulla on either side of the stylohyal fossa such that there is a distinct excavation in the paracondylar process that forms the posterior edge of the stylohyal fossa.

The external acoustic meatus is very long (it exceeds the mediolateral width of the remainder

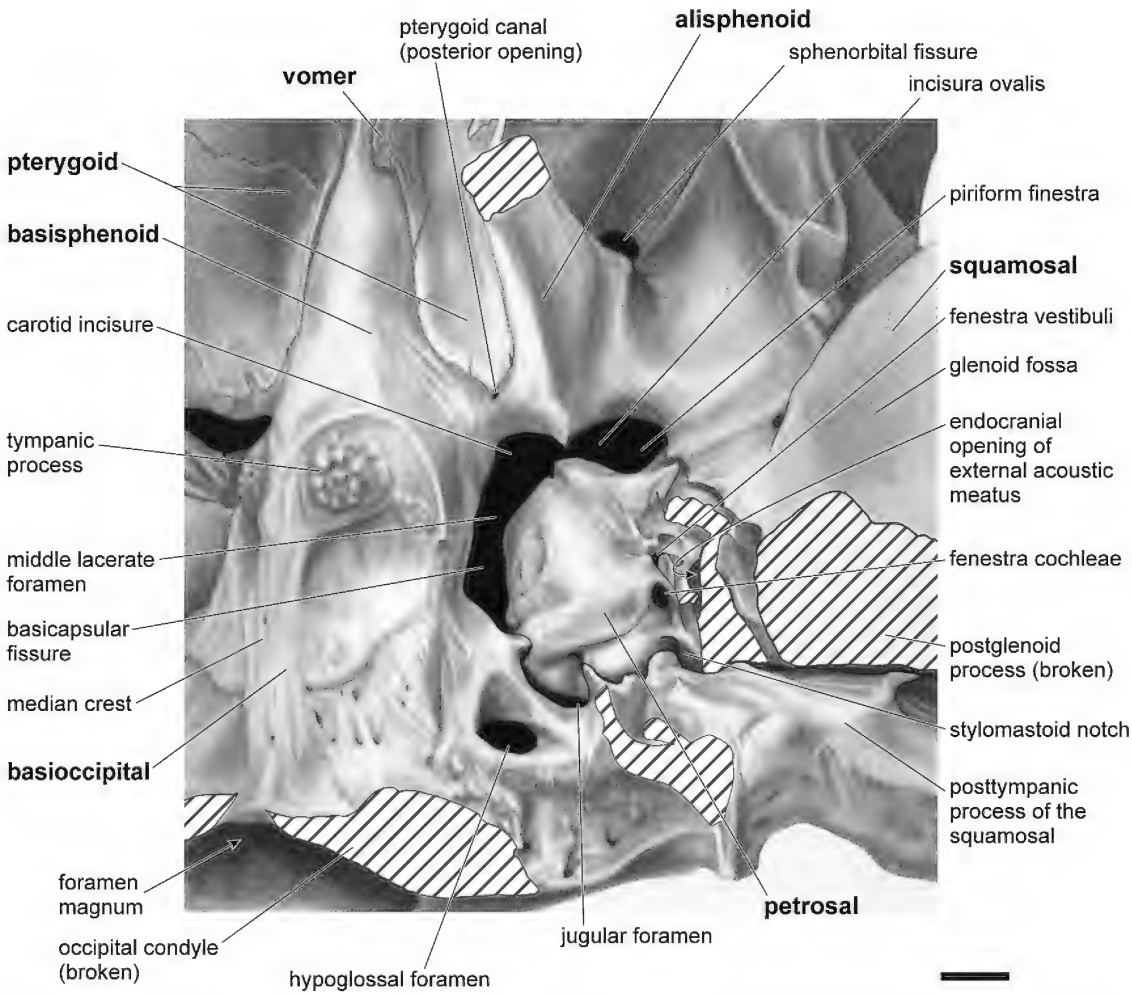

FIGURE 22. Left basicranium of *Hippopotamus amphibius* (Cetancodonta, Hippopotamidae, USNM-M 182395) with auditory bulla removed to reveal petrosal in situ. Scale bar = 1 cm. Artist: U. Kikutani.

of the bulla) and it wraps up the lateral side of the skull such that the porus acusticus externus is not visible in ventral view of the skull (fig. 21). As noted above, there is extensive fusion between the squamosal and the external acoustic meatus, however, the postglenoid and posttympanic processes of the squamosal do not fully meet ventrally; they are separated by a narrow, mediolaterally oriented slit that exposes the external acoustic meatus. Medially, the anterior and posterior carotid foramina are both set so deeply between the bulla and the petrosal that their positions can be approximated only when the bulla is in situ (fig. 21). The path to the anterior carotid foramen is the clearer of the two and is marked by a jagged-edged furrow on the bulla. The opening of the auditory tube between the bulla and petrosal is directly superior to the styliform process and is marked by a semicircular furrow in the bulla. This furrow has a sharp, crestlike lateral edge (fig. 18).

While the bulla is tightly held to adjacent bones via the external acoustic meatus laterally, on the anterior, medial, and posteromedial sides, it does not contact the surrounding squamosal, alisphenoid, basisphenoid, and basioccipital (fig. 21). The bulla is separated from each of these bones by several millimeters (note that in fig. 21,

the styliform process of the bulla partially obscures a view of this continuous space between the bulla and the alisphenoid), and the petrosal is partially visible, even with the bulla in place. The bulla contacts but does not fuse to the pars cochlearis of the petrosal. When the bulla is removed its cancellous inner structure is visible. The ectotympanic ring extends slightly more than 180° with no differentiation where the two crura meet. The auditory tube is marked by a groove on the medial bulla but the carotid foramina leave only indistinct markings.

This lack of contact between the petrosal-bulla complex and surrounding bones produces essentially one large opening that allows passage into and out of the middle ear/neck region and endocranium. Laterally the piriform fenestra lies between the petrosal/bulla posteriorly and the alisphenoid/squamosal anteriorly (figs. 21, 22). It is elongate and oriented anteromedial to posterolateral. The incisura ovalis makes a gentle indentation into what is probably the alisphenoid (although, as noted above, this should be interpreted with caution because the suture with the squamosal is obliterated). The carotid incisure, like the incisura ovalis, is visible even with the bulla in place. The carotid incisure is fully confluent with the middle lacerate foramen and the basicapsular fissure. Posterior to the basicapsular fissure a prong of bone from the exoccipital contacts but does not to fuse to the petrosal, thereby forming only a partial barrier between the basicapsular fissure and the jugular foramen. The jugular foramen is a large, squarish opening. Without the bulla in place the stylomastoid notch is indistinct but lies anterolateral to the jugular foramen. There is no exposure of the mastoid region of the petrosal on the ventral, posterior, or lateral aspects of the skull.

The glenoid fossa is rectangular to oval shaped and runs from anterolateral to posteromedial (fig. 21). The preglenoid process is absent. The surface of the postglenoid fossa is flat to convex in its center and the plane of the fossa faces posteriorly. At the lateral margin of the fossa is an elongate concavity. The postglenoid process lies primarily at the medial extreme of the joint and is a mediolaterally elongate ridge. A medial glenoid pit is absent. There is no conspicuous postglenoid foramen, but it is difficult to see the posterior aspect of the postglenoid process due to the proximity of the posttympanic process. There is a deep fissure where the postglenoid and posttympanic processes surround the external acoustic meatus anteriorly and posteriorly respectively. I cannot rule out the possibility that there may be a small postglenoid foramen contained within this space. Orliac et al.'s (2014) micro CT–based reconstructions of the postglenoid foramen in *Hippopotamus* showed that patent openings do exist in the area just noted, however, these are quite small and deep.

COMPARATIVE ANATOMY

Here I discuss comparative basicranial anatomy in the context of two recent combined-data phylogenies that include living and fossils species: the first by O'Leary et al. (2013), who sampled broadly across the orders of Placentalia for over 4000 phenomic characters as well as molecular sequence data, and the second by Spaulding et al. (2009), who sampled more living and extinct species within Artiodactylamorpha, including all those described here, but for fewer phenomic and molecular characters. The characters of Spaulding et al. (2009) were also incorporated into the broader O'Leary et al. (2013) study, and basicranial variation described above contributed many characters to both papers. Optimizations of some of those characters are discussed below and were conducted under parsimony in Mesquite (Maddison and Maddison, 2005) using matrices and trees from both of these studies (all data available on MorphoBank). Patterns discussed below summarize some of our current knowledge about particular character systems, however, a more definitive interpretation of the patterns of evolution in artiodactylan basicranial anatomy awaits the addition of more fossil and living species to the extensive character sample in the O'Leary et al. (2013) matrix.

Skull base and the separation of petrosal-bulla complex from surrounding skull: Contact between the auditory bulla and the basioccipital, and the nature of that contact (Spaulding et al., 2009: char. 84), are features that exhibit homoplasy among artiodactylans. Contact or very close approximation between the bulla and the basioccipital emerges as the primitive condition for Artiodactyla in the matrix of Spaulding et al. (2009) and is retained in *Tragulus*, *Tayassu*, *Babyrousa*, and *Camelus*. Bullar-basioccipital contact was found to be a synapomorphy of Artiodactyla by O'Leary et al. (2013: char. 897), however, as suggested by Spaulding et al.'s (2009) results, inclusion of more fossil diversity may impact this pattern. This contact is, however, lost repeatedly, including in several members of Ruminantia and in Cetacea and Hippopotamidae. Loss of contact is not a synapomorphy of Cetancodonta because contact is present in several fossil stem species that are members of Cetancodontamorpha (Spaulding et al., 2009). In some cases (i.e., *Bos*, *Potamochoerus*), the bulla lies immediately adjacent to the basioccipital but does not actually contact it. Because contact among bones in this region has been attributed functional significance (e.g., Luo and Gingerish, 1999), it is noteworthy also that extant and some fossil perissodactyls also lack basioccipital-bullar contact (Spaulding et al., 2009; O'Leary et al., 2013), phylogenetic variation that should be considered when evaluating functional hypotheses.

The bulla may also contact the overlying petrosal (O'Leary, 2010; Spaulding et al., 2009, chars. 39–42)). The anterior, medial, and posterior aspects of the bulla contact the petrosal without fusion in almost all taxa examined here except *Camelus*. In *Camelus* contact between the bulla and petrosal are absent because the basioccipital and squamosal intervene between the bulla and petrosal, and the auditory bulla fuses to those bones. The presence of contact is primitive for Artiodactyla and widespread among outgroups.

Another feature of interest deeper in the skull and visible when the bulla is removed is whether the anterior and medial parts of the pars cochlearis of the petrosal are consistently separated from the surrounding skull base. The pattern of contact for the petrosal is distinct from whether the bulla was in contact with the skull base or not. Separation of the petrosal from the skull base is typically widest between the petrosal and the alisphenoid, basisphenoid, and basioccipital. As noted or illustrated in a number of other anatomical publications on extant artiodactyl species (or closely related subfossils) described here (Kampen, 1905; Sisson, 1911; Getty, 1975; Schaller, 1992; Orliac, 2013; Rakotovao et al., 2014), many of the taxa examined have significant space between the petrosal and the carotid foramen/incisure and the foramen ovale/incisura ovalis such that these foramina are only identifiable as notches in the skull base that are fully confluent with adjacent openings. Contact between this part of the petrosal and skull base is primitive for Artiodactyla (Spaulding et al., 2009: 86) but is lost numerous times among terrestrial artiodactylans, and, notably, within Cetaceamorpha.

Separation of the auditory bulla and the petrosal from the surrounding skull base has been interpreted as having functional significance for cetaceans, which are phylogenetically nested among artiodactylans (Luo and Gingerich, 1999; O'Leary et al., 2012; Orliac et al., 2014). Isolation of the ear region from other bones has been hypothesized to enhance directional hearing underwater (Luo and Gingerich, 1999). Hippopotamids and cetaceans show both separation among ear region bones and pachyostosis of those same bones (Luo and Gingerich, 1999; O'Leary et al., 2012; Orliac et al., 2014). However, other artiodactylans show separation of ear region bones unaccompanied by pachyostosis or aquatic lifestyles, thus the functional interpretations of this character system may be more complex. The homoplasy present in the petrosal/bullar relationship to skull-base bones, suggests that there may be alternative functional explanations to explore other than aquatic hearing that would result in a separation between the petrosal and skull base. Janis and Scott (1987: 6,

table 1) observed that Pecora, or the clade of ruminants that excludes Tragulidae, is united by a "jugular foramen confluent with posterior lacerate foramen" (the latter is most likely the basicapsular fissure of O'Leary et al., 2013). I have observed, however, that this distinction may be ambiguous. The pecorans described here, *Bos taurus* and *Odocoileus virginianus,* have very close or full approximation of the petrosal to the basioccipital, almost creating separation between the basicapsular fissure and the jugular foramen. Likewise, in *Tragulus javanicus* these two foramina are partially confluent, although I note that the specimen described was slightly immature and that could affect bone position. More sampling of the variation in this area is necessary to clarify how variable this feature is.

In step with the general opening up of the cranial base, another major cranial foramen, the foramen ovale, does not always form a complete, well-defined opening in many of the species examined here. While the foramen ovale is complete in the ruminants sampled here, among the Suina and the Hippopotamidae, and *Lama,* the foramen ovale is confluent with surrounding openings such as the piriform fenestra and the carotid foramen (Spaulding et al., 2009: char. 98). As noted previously (Edinger and Kitts, 1954; Spaulding et al., 2009), absence of an enclosed foramen ovale occurs in extant Perissodactyla. Spaulding et al. (2009) showed that an enclosed foramen ovale is primitive for Artiodactyla as well as for Artiodactyla + Perissodactyla, a pattern that pertains in part because of the condition in fossil taxa and their positions on the trees. In O'Leary et al. (2013), which had fewer fossil euungulates, absence of an enclosed foramen ovale optimized as an ambiguous synapomorphy of crown Euungulata.

Another skull-base landmark, the tympanic processes (Spaulding et al., 2009: chars. 103–106) tend to be present in most taxa examined here but are quite variably developed. All the taxa described here have tympanic processes, but in the ruminants, and *Bos* in particular, they are very well developed. These landmarks tend to be positioned at the lateral edge of the basioccipital and do not make contact with the bulla in the species described here. They tend to be shaped as a bump and not a plate as in some Cetaceamorpha (Luo and Gingerich, 1999).

Kampen (1905) also noted differences in the shape of the bulla between suids, which have relatively dorsoventrally elongate auditory bullae that extend conspicuously inferior to the glenoid fossa, and tayassuids, which do not. In the hippopotamids the ventral expansion of the bulla is also absent, though it is present in camelids and ruminants.

Length of the external acoustic meatus: A relatively large external acoustic meatus (compared to the size of the rounded medial aspect of the auditory bulla) is present in almost all terrestrial artiodactylans (Spaulding et al., 2009: chars. 71–72). *Tragulus* is the only extant terrestrial artiodactylan described here for which the meatus is relatively short. Elongation of the meatus is particularly extreme in members of the Suina but also occurs in *Bos* and in *Hippopotamus.* In Suina the porus acusticus externus is positioned very superior relative to the middle ear itself.

Despite being phylogenetically nested among other Artiodactyla, fossil and living cetaceans do not have significant external expansion of the ectotympanic ring into an elongate external acoustic meatus (Luo and Gingerich, 1999), nor does the early fossil artiodactylan *Diacodexis pakistanensis* (Russell et al., 1983). The shared lack of such ectotympanic ring expansion contributed to the placement of *D. pakistanensis* in the somewhat unconventional phylogenetic position along the Cetaceamorpha stem lineage to Cetacea in Spaulding et al. (2009). Even the ectotympanic of *Tragulus* has more lateral expansion than is seen in either *Diacodexis pakistanensis* or cetaceans. A relatively elongate meatal tube also characterizes members of Perissodactyla (Spaulding et al., 2009); thus, there is homoplasy in this aspect of bullar morphology across the clade Euungulata as a whole.

In many artiodactylans there is contact between the meatal tube and the postglenoid process

(Spaulding et al., 2009: char. 80). However, in several notable exceptions figured here, this contact is lost. In Pecora, such as *Bos* and *Odocoileus*, the meatal tube is distinctly independent from the postglenoid process even though the bulla is fused to the squamosal in *Bos*. Loss of this contact also occurs in *Hippopotamus*, *Tayassu*, and *Camelus* and thus does not exhibit a particularly strong taxonomic or functional trend.

Characteristics of the auditory bulla: I have observed a sharp ridge on the auditory bulla running anteromedially to posterolaterally and marking its ventral extreme (Spaulding et al., 2009: char. 61). The appearance of this structure shows a great deal of homoplasy: it is present in *Camelus*, Suina, Hippopotamidae, and most ruminants (with the exception of *Odocoileus*). This feature is not a synapomorphy but makes multiple independent appearances across the clade, including an appearance in the cetacean *Balaenoptera* (Spaulding et al., 2009).

The size and exposure of the tympanohyal relative to the bulla is also quite variable (Spaulding et al., 2009: char. 73). Among members of Ruminantia and *Camelus* the large tympanohyal is conspicuous within the stylohyal fossa on the auditory bulla and is readily observed. Among the Suina and the Hippopotamidae, the tympanohyal is inconspicuous and completely out of view relative to adjacent bullar structures. The latter similarity is convergent given the tree topology in Spaulding et al. (2009) and O'Leary et al. (2013). However, the condition of having a small and inconspicuous tympanohyal is a shared derived feature between hippopotamids and Cetacea (Spaulding et al., 2009).

Several species described here have a highly cancellous internal structure to the auditory bulla. A cancellous bulla is present in *Camelus* and in the Suina. Among ruminants, a cancellous bulla is found in *Tragulus javanicus* and *Bos taurus,* but is absent in *Odocoileus virginianus*. A cancellous bulla also characterizes the Hippopotamidae. Extending from the bulla, a styliform process of some kind is widely present among terrestrial artiodactylans, but a particularly large one occurs in some members of Ruminantia sampled here (Spaulding et al., 2009: char. 50; note Spaulding et al.'s scoring considered a small styliform processes "absent" [e.g., in *Choeropsis*] in contrast to the description here and O'Leary et al., 2013). Across Euungulata, a styliform process also appears in perissodactyls (O'Leary et al., 2013). *Tragulus*, with its small styliform process, is an exception to the pattern seen in Ruminantia.

New dissection-based research has focused on the anatomy of the internal carotid artery as it relates to the auditory bulla and other osteological structures of the basicranium (Fukuta et al., 2007; O'Brien, 2015). These authors have shown that among Tragulidae (Ruminantia) the internal carotid artery is complete and a significant part of blood supply to the brain. Such a pattern is common in many mammals but absent in Artiodactyla. Instead, many Artiodactyla (including cetaceans and *Hippopotamus*) that have been dissected, have been shown to lack an internal carotid artery in the adult and instead to have a carotid rete mirabile epidurale, a meshwork of intracranial arteries supplying the brain (Chapman, 1881; Geisler and Luo, 1998; Fukuta et al., 2007; O'Brien, 2015). The illustrations here of *Tragulus* (fig. 16) illustrate the observations made by O'Brien (2015) that the patent internal cartoid artery in this taxon will leave a groove on the medial surface of the auditory bulla. O'Leary et al. (2013: char. 4422) showed that presence of this carotid rete was an ambiguous synapomorphy for Artiodactyla. It is important to note, however, that the optimization was ambiguous only because the representative of Camelidae (i.e., *Lama*) scored by O'Leary et al. (2013) had missing (unknown) data for the rete, although the rete has been reported for other members of Camelidae (Zguigal and Ghoshal, 1991; Ocal et al., 1998). Thus, the conservative hypothesis based on current data is that presence of the rete is a synapomorphy of the Artiodactyla, that the rete is primitive for Ruminantia, and that it was secondarily lost in Tragulidae. This pattern means that the presence of a patent, well-developed internal carotid artery in Tragulidae is not

plesiomorphic simply because it looks like the widespread condition among other mammals, but is a secondary acquisition.

Glenoid region: O'Leary et al. (2013: char. 503) found the presence of a preglenoid process to be the primitive condition for Artiodactyla, however, Spaulding et al. (2009: char. 75) found the opposite when more fossils are included. A preglenoid process occurs in the extant members of Ruminantia, Suina, and Camelidae described here. The only clades here for which the preglenoid process was not present are Hippopotamidae and *Tragulus*. For ruminants that have this feature it tends to be a low bump/plate; for Suina and *Camelus* it is an elongate ridge. The position of the preglenoid process is typically at the middle of the joint, but in *Tayassu* it is on the lateral edge of the joint, and in *Choeropsis* it is at the lateral edge of the joint. Loss of this process is a synapomorphy of Cetancodonta in O'Leary et al. (2013), however, with more fossil species included, as in Spaulding et al. (2009), the optimization is more ambiguous.

The presence of a postglenoid process is widespread among Artiodactyla, including Cetacea, and is primitive for both Artiodactyla and Euungulata (Spaulding et al., 2009: chars. 78–79). Spaulding et al. (2009) considered the postglenoid process to be absent in *Tragulus*, but here I describe it as present, just extremely gracile. Most typically this process is positioned at the medial edge of the joint, although in two cases in the taxa figured here (*Camelus* and *Odocoileus*) the process extends across the entire joint.

O'Leary et al. (2013: char. 555) showed that the presence of a posttympanic process is widespread across Mammalia and typically primitive for most mammalian clades, including Euungulata. In taxa the posttympanic process is a distinct knob or ridge that projects ventrally. Pearson (1927) identified a posttympanic process even though it may take a different, platelike shape in species such as tayassuids and relatives, which, incidentally also have extensive fusion in this area of the skull among the squamosal, ectotympanic, and exoccipital bones that makes the boundaries of bones hard to delineate. Thus, there is distinct variation in the shape of the squamosal as it descends posterior to the ectotympanic and in whether it forms a distinct process or not. To reflect the non-knoblike shape of this area in species like *Sus,* I scored the posttympanic process as absent (O'Leary et al., 2013), a concept that differs from the Pearson's (1927) definition. Spaulding et al. (2009) reported that fusion of the postglenoid and posttympanic processes of the squamosal occurred only in Suina (Spaulding et al., 2009: char. 81) among taxa sampled here. When this fusion occurs the ectotympanic portion of the external acoustic meatus may be obscured by the squamosal to which it is highly fused.

Presence of a postglenoid foramen is the primitive condition for Artiodactyla (Spaulding et al., 2009, char. 89), but it is also a structure that disappears in some clades within Artiodactyla. Spaulding et al. (2009) found that loss of the postglenoid foramen is a synapomorphy that appears on the tree within Cetancodontamorpha. Thus, the absence of this foramen among extant members of Suina is a convergent condition. The postglenoid foramen is often situated completely within the squamosal (e.g., *Odocoileus*, *Tragulus*), but it is occasionally found between the squamosal and the exoccipital (e.g., *Bos*, *Camelus*). A feature of some ruminants illustrated here is that a bar of bone divides the postglenoid foramen into two foramina, and the collective opening becomes relatively large in such situations. This configuration also occurs in *Camelus*. *Tragulus* has a distinctly small postglenoid foramen, an observation also made by Webb and Taylor (1980). Regarding the adjacent stylomastoid foramen, presence of a sulcus external to the stylomastoid foramen (Spaulding et al., 2009: char. 93) occurs in Hippopotamidae (as well as in some other cetancodontans not illustrated) and *Bos*. According to Spaulding et al. (2009), the presence of this sulcus is a synapomporphy that comes on the tree within Cetancodontamorpha.

Occipital region: In the occipital region, some form of flexion stops on the occipital con-

dyles (Spaulding et al., 2009: char. 115), convexities at the anterior aspect of the condyle (Janis and Scott, 1987), characterize all the ruminants examined. Janis and Scott (1987) emphasized that flexion stops are best developed among species of Pecora. This observation is supported by the illustrations here. Absence of flexion stops is primitive for Artiodactyla and Euungulata. A parallel development of flexion stops in Ruminantia occurs in *Camelus*. The condition of having occipital condyles that contact each other in the midline (Spaulding et al., 2009: char. 167) occurs only in *Camelus* among species examined here. A median occipital ridge (Spaulding et al., 2009: char. 177) does appear to be primitive for Artiodactyla but shows homoplasy in being absent in *Odocoileus* and in many members of Suina.

The paracondylar process of the exoccipital varies in size (Spaulding et al., 2009: char. 182, where it was referred to as the *paroccipital process*) among the taxa examined here and extends below the ventral margin of bulla. The primitive condition for Artiodactyla is that this process does not extend inferior to the bulla. However, in Ruminantia, except *Tragulus*, the paracondylar process is much longer and often extends conspicuously inferior to the bulla. This secondarily elongate condition also occurs in *Babyrousa* and *Potamochoerus*, but not in *Sus*, as has been previously noted (Pearson, 1927). Contact between the paracondylar process of the exoccipital and the adjacent auditory bulla (O'Leary et al., 2013: char. 917; not a character in Spaulding et al., 2009) is a synapomorphy of Artiodactyla and contact is widespread among the taxa sampled here, absent only in *Tayassu*. This pattern should, however, be reexamined after the inclusion of more fossil species in the O'Leary et al. (2013) matrix.

CONCLUSIONS

I provide an illustrated description of key exemplar species that represent anatomical variation among extant members of Artiodactyla living in terrestrial (Camelidae, Ruminantia, Suina) or semiaquatic (Hippopotamidae) habitats. This contribution complements recent descriptions of the comparative anatomy of cetacean skulls (Luo and Gingerich, 1999; Mead and Fordyce, 2009) and artiodactylan petrosals (O'Leary, 2010 Orliac, 2013; Orliac and O'Leary, 2014; Orliac et al., 2014) and provides an additional resource for anatomical terminology and homology for ongoing phylogenetic comparisons. Separation of the petrosal and bulla from the surrounding bones of the skull base in living and fossil cetaceans has been hypothesized to relate functionally to the derived behavior of processing sounds underwater. Among noncetacean artiodactylans, only the semiaquatic Hippopotamidae have a broadly similar configuration of the basicranium wherein the pars cochlearis of the petrosal and the auditory bulla are both separated from the rest of the skull by space. However, because this separated condition also occurs in outgroups such as *Equus*, further examination of the function of this condition and its relation to underwater hearing should be explored.

Among fully terrestrial and semiaquatic artiodactyls, the pars cochlearis of the petrosal tends to be separated from the rest of the skull base but not necessarily the underlying auditory bulla. Accompanying the separation of the pars cochlearis is a tendency for a number of cranial foramina such as the piriform fenestra, foramen ovale, carotid foramen, middle lacerate foramen, and basicapsular fissure to become confluent. There is also considerable variation in the position and length of the external acoustic meatus among these taxa. All of them have some expansion of the external acoustic meatus laterally from the ectotympanic ring, and this expansion may be positioned relatively superiorly on the lateral side of the skull.

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On the cover: Basicranium of *Tragulus napu*.